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# THE MORPHOLOGY AND DEVELOPMENT OF THE WING PATTERN OF LEPIDOPTERA

By ERNST CASPARI

*Fellow of the John and Mary R. Markle Foundation, Lafayette College*

## INTRODUCTION

THE surface pattern of animals involves important questions for several branches of biology. Taxonomists often use pattern features for distinguishing between species. Some pattern formations have a definite ecological value, and the imitation patterns, e.g., the leaf imitations by the wings of different kinds of butterflies, have played an important rôle in the discussions about natural selection. On the other hand, the developmental implications of pattern formation have a bearing on many problems of general developmental physiology. Goldschmidt called attention to the fact that all developmental processes may be regarded as pattern formations, i.e. the creation of differences in a previously uniform material. The wing pattern of Lepidoptera seemed to him an extremely convenient material for the analysis of developmental questions, since it is two-dimensional only and develops in relatively late stages of life. Also, since it is of only minor importance for the life of the organism, operations can be easily executed.

In the actual analysis of the wing pattern of Lepidoptera investigators have tried to follow all these suggestions. The analysis has succeeded in a singular way in combining the methods of comparative morphology, of genetics, and of experimental embryology. In this way a certain part of the pattern problem in Lepidoptera has already been solved, giving major contributions to problems of general importance, such as the action of genes, the resemblance between gene effect and modification and the determination process.

## DESCRIPTION OF PATTERNS

### *The pattern of Philosamia cynthia*

The first task of pattern analysis consisted in giving an adequate description. The first important step was made when Schwanwitsch (1924) and Sueffert (1925, 1927) showed that the wing pattern of butterflies and moths must not be regarded as a whole, but must be divided into several independent *systems*.

Pattern elements are regarded as belonging to the same system, when, from one species to another, they are found to vary



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concomitantly and independently of other pattern elements. The same concomitant variation of pattern elements belonging to the same system is found in individual fluctuations within a single species, as Henke (1928) has shown in a population of *Larentia sordidata* (Geometridae.)

In many species two transverse bands are found crossing the wing. Each band may be composed of one color only, or of two or even three differently colored stripes, as in the case of the Ailanthus silk-moth, *Philosamia cynthia* (Fig. 1), which has been analyzed by Henke (1933). In this species, the three colors of the band are black, white, and pink, and it appears clearly that the colors in the two bands are symmetrically arranged about the field which lies between the bands: in each case black is the innermost stripe, pink the outermost one. Therefore, the bands have been called "symmetrical bands" (Sueffert). The area they surround has a somewhat darker coloration than the two fields bordering the bands at the outside and at the base of the wing, and it is therefore designated as the "central field" (discal area) in distinction from the "outer-fields," which embrace the "external field" (post-discal area) distally and the "internal field" (basal area) proximally. Both outer-fields have the same coloration. The central field and the bordering bands together are called the "symmetrical system."

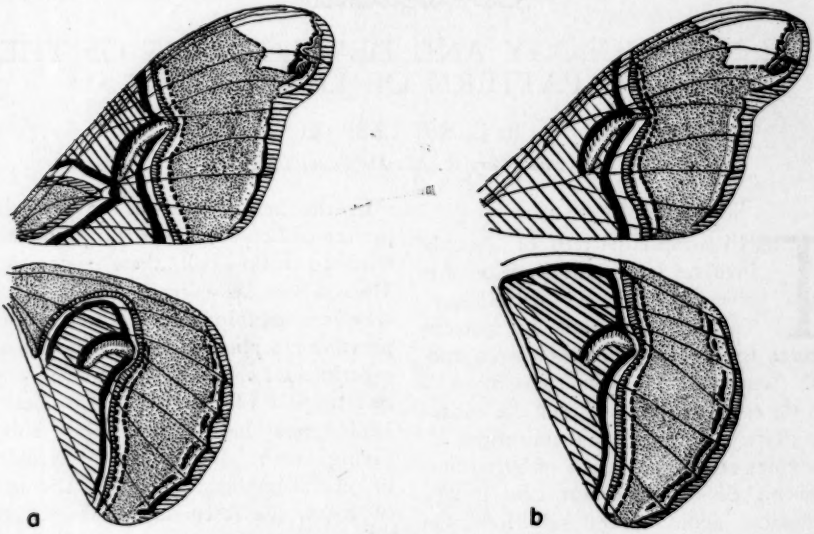


FIG. 1. SCHEME OF THE WING PATTERN OF PHILOSAMIA CYNTHIA
(a) upper side; (b) under side. Simplified after Henke (1936)

Another element, almost constantly found in Saturnids and often among other Lepidoptera is characterized by its situation on the transverse discal vein, the discocellulus, or when this vein is lacking in the adult moth, as in *P. cynthia*, between the cubital and medial vein systems (Henke 1933). In Saturnids it often forms an ocellus, consisting of differently colored bands. In *P. cynthia* it is extended forming a crescentic spot, which, how-

ever, still shows the differentiation into different bands characteristic of the typical ocellus. Its center lacks scales almost completely, and the bare epithelium has a glasslike appearance. The center is surrounded by a white line which is followed by a yellow one. Following closely the shape of the ocellus outside of the yellow stripe, a black line is found at the fore edge of the ocellus only, and is in direct connection with the black stripe of the symmetrical bands.

Whereas the internal field of *P. cynthia* is homogeneous, the external field shows several differentiations. Closely attached to the external zone of the distal symmetrical band a long area appears, not well defined against the external field but distinguished from it by its lighter color—the so-called "external shadow."

Near the tip of the wing a lilac area is found, the "apical patch," which is bordered distally by a clear-cut white line, the "apical line." An ocellus, dark in Fig. 1, which is lying on its inferior margin, seems to belong to the same system, but comparison with other species reveals its complex origin. Only the innermost white stripe is a continuation of the apical line. The outer dark part belongs to the outer-field, whose boundary against the marginal elements may be marked by a band of dark scales.

In the marginal area of the wing, the borderline, running parallel to the wing margin, divides the distal "marginal field" from the more proximal "border-field," which again is clearly distinguished from the external field by its lighter coloration. This boundary of the border-field against the external field is marked in many species by a distinct band, whose topmost part is encountered in *P. cynthia*, forming the above-mentioned part of the apical ocellus.

### *The general type of wing pattern of the family Saturnidae*

In the same way, the wing pattern of many Lepidoptera has been described. If only a certain group of related species is considered, comparable elements in different species are found. By comparing a large number of species and proceeding from group to group, it has been possible to develop schemes containing all pattern elements occurring in a certain family, i.e. a *general type* for the wing pattern of this family. Schwanwitsch and Sueffert first suggested independently a type for the wing pattern of Nymphalids, and the striking similarity of those two

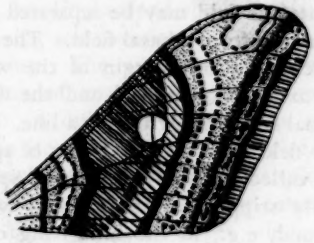

FIG. 2. GENERAL TYPE OF THE WING PATTERN OF SATURNIDS
After Henke (1935)

attempts forms strong evidence for the reliability of the method. Henke proposed a scheme for the wing pattern of Saturnids which will be more extensively described as the physiological analysis in Saturnids has proceeded comparatively far (Fig. 2).

Many of the elements found in this scheme have already been encountered in *P. cynthia*. The two dark bands across the wing represent the symmetrical bands, including the hatched central field. Inside the central field, the colorless ocellus and a heavily hatched band, the central shadow, are indicated in the figure. The part of the central field proximal to the central shadow has been represented by

another kind of hatching, indicating that this field in some species is distinguished in coloration from the distal part of the central field. The outer-fields on both sides of the central field, the external field and the internal field, are dotted in the same way in the drawing, in order to show that they are colored alike. The external field may contain an external shadow (colorless in the drawing), and the internal field sometimes exhibits a corresponding internal shadow. At the tip of the wing the apical patch is represented by a colorless area, bordered at the distal side by the apical line. The boundary of the external outer-field against the border elements may be marked by a line or band. The internal field may be separated in a similar way from a basal field. The two fields close to the margin of the wing, the proximal border field and the distal marginal field, are divided by a line. The border field may contain a row of spots, the so-called "pseudo-submarginal spots" (heavily stippled in the sketch) which are found, e.g., in the hind-wing of *P. cynthia* (see Fig. 1).

It must be emphasized that several elements of minor importance have been omitted in this sketch, namely several fields which never form border elements but only cause minor variations of coloration in the areas they cover, some rhythmical pattern elements, and some elements dependent on the structure of the wing, e.g., a distinguishing coloration of the veins.

Starting from this scheme every wing pattern occurring among Saturnids can be derived. In all special cases only a part of the possible elements is developed, while others are lacking. Furthermore, the elements which occur may be differently developed and differently colored in different species.

A band may consist of one color only, or of two or even three differently colored stripes. It may be constricted at the level of a vein or even dissolved into a row of spots. A band may be interrupted at the level of a vein, while the other part of the band is displaced and continues for a certain distance proximally or distally from the same vein, a phenomenon to which Sueffert has applied the geological term "dislocation." A special case of dislocation is the so-called "pierellisation," first described by Schwanwitsch in the genus *Pierella*. In this case, parts of different bands are displaced in such a way that they form new lines which seem a unit at first sight but which are in fact composed of parts of morphologically different bands (Fig. 3).

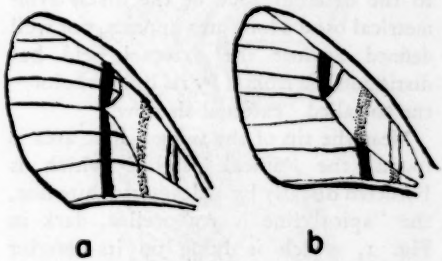


FIG. 3. PIERELLISATION OF TRANSVERSE BANDS IN THE GENUS PIERELLA

(a) typical pattern; (b) formation of combined bands by means of dislocations. From Henke (1935) after Schwanwitsch.

Pierellisation, on the other hand, illustrates the fact that parts of different morphological origin can combine into an optically uniform entity, as has already been shown for the apical ocellus in *P. cynthia*. The occurrence of this phenomenon is a special case of the principle, first investigated by Henke (1936), that pattern elements often prefer a certain position on the wing, and that at such places several elements of different morphological value may be encountered very close and parallel to each other, like

the external shadow of *P. cynthia* which lies exactly parallel to the symmetrical band. In other cases, two different pattern elements may even cover each other so that they cannot be distinguished. In normal *P. cynthia* specimens, for example, no internal shadow can be found. However, in abnormal specimens, in which the central field is reduced in size and the symmetrical bands are nearer each other than in the normal case, a clear internal shadow at the ordinary place of the proximal symmetrical band is seen. This suggests that it is ordinarily present

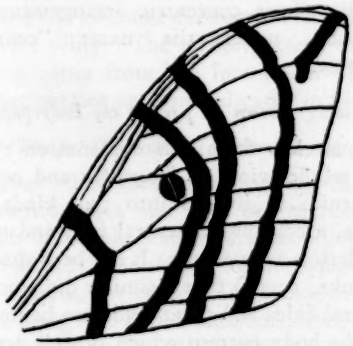

FIG. 4. MAIN PATTERN LOCI FOR THE WING PATTERN OF SATURNIDS
After Henke (1936)

but covered by the proximal band (Henke, 1936). Quite a few instances of close parallelism or even partial or complete overlapping of different pattern elements suggested the conclusion that certain areas of the wing, *pattern loci* (Henke), are most likely to contain pattern elements. Fig. 4 shows the chief pattern loci of the Saturnid wing.

### *The wing of P. cynthia considered as a tridimensional object*

The upper side of the hind-wing and the under side of both wings show pattern elements similar to those on the upper side of the fore-wing. A close examination of those patterns in *P. cynthia* led to new points of view (Henke 1933b). The upper side of the hind-wing possesses a symmetrical system like that of the fore-wing, with the difference that the proximal and distal symmetrical bands unite anteriorly (see Fig. 1). In this way the central field does not reach the foremost edge of the wing, but is open towards the hind border of the wing only. The same is true for the under side of the hind-wing, so that the central fields of upper side and under side are in connection at the hind edge of the wing only. It seems justifiable to consider the central field of upper side and under side as one continuous field, bending around the hind margin of the wing and covering it in the manner of a clamp. The whole system would be surrounded entirely by the symmetrical band. A difficulty of this view appears in the fact that the proximal band of the under side reaches the hind margin somewhat nearer the base than the corresponding band at the upper side. Close inspection of the hind margin of the wing, however, reveals that both bands are connected by a narrow line of white scales following exactly the hind margin of the wing. If it is kept in mind that the wing actually is a tridimensional object, consisting of a bag of epithelium evaginated from the body surface, it is clear that a part of this epithelium, the central field, which covers part of the upper surface as well as the under side of the wing is entirely surrounded by a line and distinguished in coloration from the surrounding outer-field.

This conception can also be applied to the fore-wing of *P. cynthia*. The under side in this case shows only the distal symmetrical band and the central field reaches the base of the wing. The proximal band of the upper side bends at the

fore and hind edge towards the base, but does not reach it. A connecting line which closes the central field, such as is present on the hind wing, cannot be found. However, even this fact fits the conception of a continuous central field on upper and under side, surrounded by the symmetrical band, if the phenomenon of dislocation is taken into consideration. It means in this case that parts of a band may be shifted against each other at the margin of the wing as well as at certain veins in other cases. This view is confirmed by the observation that under experimental conditions a proximal band may appear at the under side of the fore-wing. Following this conception, the central field of the fore-wing constitutes a large band wound around the whole wing, having a constriction in the middle of the upper side. Under certain conditions it can be divided at the level of this constriction in such a way that an incompletely closed band appears around the whole wing. In this case two independent central fields seem to be present at the upper side, both surrounded by a symmetrical band and open against one of the edges of the wing. In Fig. 5, a tridimensional scheme for the wing pattern of *P. cynthia* is given, the wings being represented by squares in which the situation of the central fields is marked. On the fore-wing, the abnormal case of a divided central field has been supposed. The central field as it is regarded here, lying on upper and under side of the wing and entirely closed from the outer-fields by the symmetrical bands, shows a concentric arrangement and therefore it has been proposed (Sueffert, 1929; Henke, 1933a) to include it together with the discal ocelli, whose concentric arrangement is obvious, under the name "centric systems."

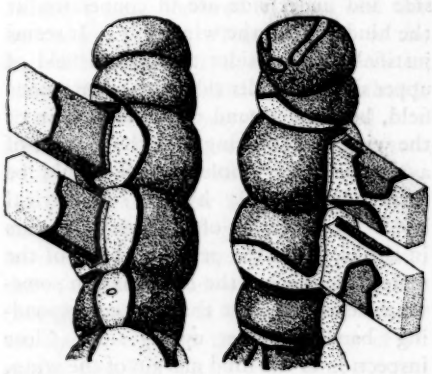

FIG. 5. TRIDIMENSIONAL SCHEME OF THE ARRANGEMENT OF CENTRAL FIELDS AND OUTER-FIELDS ON THE WINGS AND BODY OF PHILOSAMIA CYNTHIA

Central fields, dark; outer-fields, light; symmetrical bands, black. After Henke (1933b).

*The wing pattern as part of the body pattern*

It is clear from this explanation that the whole wing of *P. cynthia* and other Saturnids is divided into two kinds of areas, a continuous central field and two bordering outer-fields. It has been shown (Henke, 1933b) that a similar division in central fields and outer-fields can be found in the body pattern which is well developed in the subfamily Attacini to which *P. cynthia* belongs. The distribution of central fields and outer-fields on the thorax and the first two abdominal segments of *P. cynthia* has been represented schematically in Fig. 5, dark shade meaning central fields and light shade the outer-fields. Actually, the decision whether a bordered field of the body of *cynthia* is a central field or an outer-field is not easily made, since the color differences between the two kinds of fields are very slight. Therefore, the differences of coloration in the different zones of the bordering bands are used as a criterion, black being adjacent to the central field and red to the outer-fields. This difference is well developed in certain moths belonging to the

genus *Rothschildia*. By comparison with those species, the decision whether a certain field of the body is to be considered as a central field or as an outer-field is reliably possible even in species like *P. cynthia*, which does not show this color difference between the zones of the borderlines in the body pattern.

In this way, the arrangement of the wing into central field and outer-fields has to be considered as a special case of the differentiation of the whole body surface, of which the wing epithelium is a part. The whole body surface is divided into two kinds of areas, central fields and outer-fields, and the same differentiation is found in the wing. The richer pattern of the wing arises from the interaction of the other pattern systems indicated in Fig. 2.

### *The field character of pattern elements*

The other elements occurring in the Saturnid wing can also be regarded as fields or as field border differentiations, as has already been shown for the symmetrical system, the symmetrical bands in this case being field border differentiations. In order to describe all occurring cases in terms of this conception, Henke (1936) has distinguished three types of boundary formation. In type I the two fields have different coloration and meet each other without border differentiations, e.g., external outer-field and border-field in *P. cynthia*. In the second type, the two fields have also different colors, and are divided by borderlines. The symmetrical system and the outer-fields of *P. cynthia* are an example of this type. In type III the borderlines divide two areas of the same coloration, so that the border differentiations seem to emerge from a uniform background. However, in an example of this type, the symmetrical system and the outer-fields of the meal moth, *Ephestia kuehniella*, differences between the equally pigmented areas appear under the influence of certain genes (Whiting, 1919; Kuehn, 1937, 1939b) and of external modifying factors (Strohl and Koehler, 1934). (See below.)

### *Adaptive patterns*

By means of the methods described a great many patterns of Lepidoptera have been analyzed, and it has been possible to reduce even very complicated ones to special cases of the general type. Special interest is found in adaptive patterns, e.g., patterns which cause the wings as a whole to resemble a leaf. Sueffert has succeeded in describing the complicated pattern of the leaf-butterfly *Kallima* in terms of the Nymphalid scheme, and Henke (1936) similarly analyzed a number of adaptive patterns in Saturnid moths. The resemblance to a leaf in all those cases is effected chiefly by a dark line crossing the wing obliquely, giving the impression of the mid-vein of a leaf. However, this line may correspond in different species to different pattern elements, e.g., distal symmetrical band, central shadow, or border of the external outer-field. Or it may even be composed of different parts of different morphological value, as distal band plus border of the external field (*Solus drepanoides*); or distal symmetrical band plus proximal band of the ocellar system (*Kallima*, Nymphalidae). The latter cases provide an instance of the phenomenon called "total pattern" by Sueffert (1925)—the collaboration of independent elements of different origin in the production of an optically uniform effect. In the case of the leaf-imitating moths it may be explained by the existence of a pattern locus that crosses the wing obliquely and which can be occupied by different elements. The problem is, however, complicated by the collaboration in some species of the hind-wing in the

production of a leaf-imitating impression. In those cases, the hind-wing too is crossed by an oblique line, corresponding to the line on the fore-wing in coloration and continuing it exactly in the normal wing position, contributing to the effect that fore- and hind-wing together look like a leaf. An explanation of the fact that two lines of different morphological value on different wings may be arranged so as to give a uniform optical effect, is not yet possible.

The pattern systems, developed by a purely morphological analysis, are considered as homologies by Schwanwitsch, and he has followed their variation from species to species and from group to group among the Nymphalids, using it as evidence for the evolutionary connection between different species. Henke, although not denying the possible importance of the study of patterns from this point of view, considers it especially as yielding evidence for comparable processes in ontogeny, and uses for this conception the term "plastology." Two formations are called plastologous, if they are originated by equivalent developmental processes. The symmetrical bands of different kinds of Lepidoptera, for example, are regarded as plastologous, implying that they are caused in the same way. In this way, the morphological findings furnish a starting point for the experimental analysis of the origin and development of wing patterns which has already proceeded considerably through the work of Kuehn, Henke and their collaborators.

The chief experimental animal for this work hitherto has been, besides *Philosamia cynthia*, the meal-moth *Ephestia kuehniella*. Its very simple pattern will be described briefly (Fig. 6). The symmetrical bands consist of three zones, of which the middle one is white, the other two being dark. The central field enclosed by the bands has the same greyish or brownish coloration as the outer-fields. Inside the central field, two kinds of elements are encountered, the central shadow and the discal element. The former is present in most of the strains in the form of four dark spots, the shadow spots. The discal element is represented by two dark "central spots" and a white spot between them. At the margin of the wing, 5 dark marginal spots are found lying between the veins.

FIG. 6. WING-PATTERN OF THE FLOUR-MOTH EPHESTIA KUEHNIELLA
After Kuehn and Henke (1929)

## ONTOGENETIC PROCESSES CONCERNED IN PATTERN FORMATION

### *The reaction of pattern systems on environmental factors*

Pattern elements belonging to the same system have been shown to react in the same direction under modifying influences. After treatment by high or low temperature at a certain time after pupation, the "sensitive period," changes in the pattern of Lepidoptera may be obtained. That every morphological system has its own distinct sensitive period was first proved by Kuehn (1926) in *Argynnis paphia*. Later on the sensitive periods of the different systems in *Ephestia* were thoroughly examined by Feldotto (1933), by Kuehn and Henke (1936), by Wulkopf (1936), and by Stubbe (1938). Feldotto, testing the effects of heat shocks, i.e. brief exposures to barely sub-lethal high temperatures (47°C.), found that at different times after pupation elements belonging to different systems react in a different way.

Elements, however, which belong to one and the same morphological system always showed deviations in the same direction (Fig. 7). After a heat shock shortly after pupation, the marginal spots increase in size, i.e. the number of dark scales forming the spot is increased. A maximum number of dark scales in the marginal spots is obtained after heat treatment at 36–48 hours after pupation. Heat treatment of somewhat older pupae has a smaller effect on the marginal spots, and following a heat shock applied 72 hours after pupation the marginal spots become even smaller than in untreated specimens. After this time, a heat shock has no effect at all on the marginal spots.

On the other hand, the dark elements of the symmetrical bands show an entirely different kind of reaction to heat. Heat treatment shortly after pupation diminishes the intensity of the dark bands, reaching a minimum at 24–36 hours after pupation. Shortly after this time, a heat shock does not influence the intensity of the bands as compared with untreated animals. But later on, at a time when heat treatment no longer affects the marginal spots, the intensity of the symmetrical bands attains a second minimum after a heat shock. After this time, the curve for the intensity of the black bands after heat treatment returns gradually in the direction to normal.

Another sensitive period has been found for the size of the central field. Following heat treatment shortly after pupation, the symmetrical bands are removed from each other, so that the central field is extended. Later on, heat treatment causes the bands to approach each other, reducing the size of the central field considerably. The maximum reduction is found following a heat shock applied 48–60 hours after pupation.

The results of Feldotto were confirmed and enlarged by Wulkopf and by Stubbe. They also established sensitive periods and characteristic reaction curves for the central shadow and the central spots. Characteristic alteration curves for the different systems were also found after a short treatment with low temperature and after a prolonged exposure to moderately high temperatures (35°C.). The effects of these influences were in some systems equal to those produced by a short

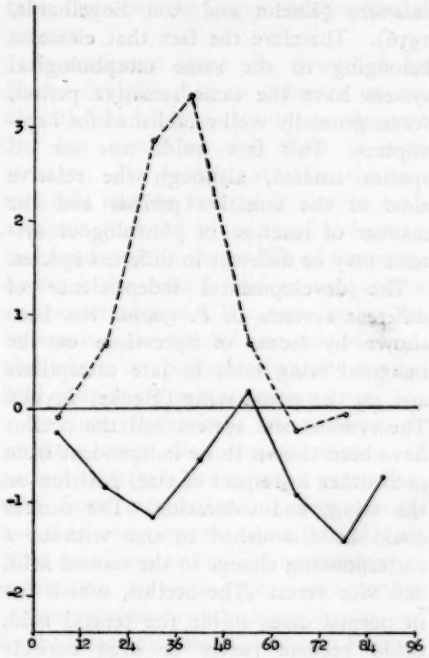


FIG. 7. SENSITIVE PERIODS OF THE INTENSITY OF THE SYMMETRICAL BANDS (——) AND OF THE NUMBER OF SCALES IN THE THIRD MARGINAL SPOT (– – – –) OF EPHESTIA KUEHNIELLA

Abscissa: age of the pupae at the time of heat treatment, in hours after pupation. Ordinate: mean of the animals treated at the respective times, expressed in standard deviations for the variation of the controls. O: mean of the controls. Positive values indicate increase, negative values decrease as compared with the controls. From Kuehn and Henke (1936) after Feldotto.

heat shock of 47°C., in other cases, however, they were different.

Comparable results have been found in experiments with *Argynnis paphia* (Kuehn, 1926), *Vanessa urticae* and *io* (Koehler and Feldotto, 1935), and *Abraxas grossulariata* (Kuehn and von Engelhardt, 1936). Therefore the fact that elements belonging to the same morphological system have the same sensitive period, seems generally well established for Lepidoptera. This fact holds true for all species studied, although the relative time of the sensitive periods and the manner of reaction of plastologous systems may be different in different species.

The developmental independence of different systems in *P. cynthia* has been shown by means of operations on the imaginal wing buds in late caterpillars and on the pupal wing (Henke, 1933a). The symmetrical system and the ocellus have been shown to be independent from each other in respect of size, position on the wing, and coloration. The ocellus could be diminished in size without a corresponding change in the central field, and vice versa. The ocellus, which lies in normal cases inside the central field, could become partly or even entirely removed from it into the external field. An operation in the early pupa affects the coloration of the symmetrical system; red scales are scattered in the symmetrical bands and in the central field, but not in the outer-field nor in the ocellus. The white zone of the symmetrical band may appear pinkish on account of the interspersed red scales, whereas the white zone of the ocellus keeps its pure white color. The outermost black stripe of the ocellus, however, behaves in this experiment like the black stripe of the symmetrical band. Therefore it must be concluded that, although its shape and position are determined by the ocellus, its coloration follows that of the symmetrical band.

Also in other cases, experiments have revealed differences between elements which in the morphological analysis first seemed to be parts of the same system. In *Abraxas* the symmetrical bands consist of three zones, a yellow line in the center bordered against the central field and against the outer-fields by a row of black spots. In the experiments of Kuehn and von Engelhardt (1936), involving alterations of temperature in the pupal stage, the outermost row of black spots showed an entirely different sensitive period from the innermost one. A similar fact has been recorded in *Ephestia* by Stubbe. The innermost dark stripe of the symmetrical bands shows a stronger reaction to a prolonged influence of a moderately high temperature than the outermost dark zone. The latter, however, reacts much more strongly to a short heat shock. In both cases, the behavior of the outermost dark stripe of the symmetrical bands resembles more that of the marginal spots than that of the innermost zone of the band. This behavior indicates that the outermost zone of the symmetrical bands does not belong originally to the symmetrical system, an assumption that will be shown below to have been proved by other experiments.

### *The reaction of pattern systems on genetic factors*

The different systems show their developmental independence also under the influence of Mendelian factors. A number of genes have been described in *Ephestia* which act on the size of the elements of one system only. There are genes influencing the intensity of the symmetrical bands (one of them sex-linked (Kuehn and Henke, 1929, 1932; Huegel, 1933; Clausen, 1937; Schwartz, 1938)), of the marginal spots (Kuehn and

Henke, 1929), of the central shadow (Clausen, 1937), and of the central spots (Kuehn and Henke, 1932) which affect the number of dark scales in the respective systems exclusively.

Other genes have a certain influence on the arrangement of scales in a certain system without affecting its size. The gene rb (Clausen, 1937) affects the shape of all marginal spots. They are broader and narrower in rbrb animals than in Rb- animals, so that they even may join each other forming an uninterrupted band at the margin of the wing. Two genes influencing the size of the central field and the position of the symmetrical bands have been found by Kuehn and Henke (1936). The dominant gene Sy (lethal when homozygous) causes the bordering bands to approach each other, diminishing in this way the size of the central field. Another factor Syb (intermediate in the heterozygote) enlarges the central field, removing the bordering bands from each other. The effects of those genes resemble the effects of heat shocks applied in the sensitive period for the size of the central field in normal animals. The effects of temperature treatment in these sensitive periods are therefore to be considered as phenocopies of the genes in question—using a term proposed by Goldschmidt. The meaning of this phenomenon in this case can be analyzed by simultaneous influence of the temperature and the genes. The experiments have shown that the actions of both these genes and of temperature treatments during the sensitive period of the corresponding regions are additive. The central field of a Sy-wing is enlarged in the direction to normal by a heat shock in the early part of the sensitive period, as well as by the presence of the gene Syb in the same animal. It is still further reduced by the influence of heat in the later part of the sensitive period. It is, however, impossible to enlarge the central field of a Syb-wing by an additional heat treatment in the early part of the sensitive period. The possibility of combining the gene effects with the modificatory influences suggests that both act on the same developmental process.

A sex-linked gene dz, described by Kuehn (1939b), has an influence on the central field which is similar to the gene Sy, but sometimes its effect is even stronger. For in dz dz-animals, the central field may be reduced in size to such a degree, that the white distal and proximal bands join in the middle of the wing, dividing the central field in an anterior and posterior part. The gene dz, besides influencing the size of the central field, also affects its pigmentation, the central field of dz dz-animals appearing sooty.

By the whole bulk of evidence, it becomes clear that the conception of pattern systems is not merely a generalization from morphological observations, but that every system constitutes a unit of its own for genetical and environmental influences. A system appears as a number of pattern elements which are determined by the same ontogenetic process. Further analysis described below will give some evidence concerning the nature of this determinative process.

It must, however, be emphasized that the independence of the different systems and the uniformity of reaction of elements belonging to the same system is not absolute. Several genes have been described in *Ephestia* which influence two systems at once. A gene found by Huegel (1933) affects at the same time the intensity of the white symmetrical bands and of the white parts belonging to the central spots. The above mentioned genes Sy and Syb, besides influencing the size of the central field, affect the situation of the central

spots on the wing (Kuehn and Henke, 1936). Schwartz (1938) described three genes which act on the expression of single bands belonging to the central system, namely the proximal internal band, the distal internal band, and the distal external band, respectively. On the other hand, Koehler and Feldotto (1935) found in *Vanessa urticae* that the sensitive periods of relatively remote parts of the same system are slightly different.

### *The determination of the central system in Ephestia*

An analysis of the process determining the shape and size of a system has been successfully started in the case of the central system. Kuehn and von Engelhardt (1933) made slight burns on the pupal wing of *Ephestia* with the aid of a microthermocautery. Three types of reaction could be sharply distinguished, depending on the time of operation. In the first period, during the first day after pupation, the effects on the wing pattern were entirely local (Fig. 8). The white zone of the symmetrical band was bent around the operation scar, so that the scar always lay in the outer-field. The external dark symmetrical band is always situated at the external side of the scar, divided by it from the white line. The other parts of the wing remote from the scar are not changed. If the defect has been set in the region of the anal vein—a vein which is found in *Ephestia* in the pupal wing, but not developed in the adult moth (Behrends, 1935)—the symmetrical field becomes divided into two parts, each bordered by a band and open to the anterior or posterior margin of the wing, resembling the cases in *P. cynthia*, which are schematically represented in Fig. 5, as well as some pictures obtained after heat treatment at the maximum of the sensitive period for reduction of the central field, or under the influence of the gene dz in *Ephestia*.

If a great number of operated wings, containing cautery marks at different points, are compared, the pictures obtained for the central system suggest a determination stream which is spreading over the wing after the time of operation and cannot pass over the scars. The border of this stream would be constituted by the white band, while the outermost dark zones lie outside of the scar and belong obviously to the outer-fields, a fact already suggested by their behavior in the temperature experiments. The course of the determination stream can be reconstructed from the pictures obtained by operating at different points. It seems to enter the upper side of the wing from the fore as well as from the hind edge. Both currents spread over the wing and meet in the anal vein region, spreading afterwards in proximal and in distal direction until they reach the usual situation of the white lines, if they are not held back by an area of cells which have been killed by the cauterization (Fig. 8k).

In the second period, 48–60 hours after pupation, an entirely different type of reaction is encountered. After an operation at this time, the whole central field is reduced in size, regardless of the situation of the defect. Different grades of this reaction are found and indicated schematically in Fig. 8—low grades of reduction, resembling the action of heat treatment in the second part of the sensitive period for the size of the central field or by the gene Sy or dz, and higher grades, in which the central field may even be divided into two parts at the level of the anal vein. If the central field is considerably reduced in size by the operation, the different parts constituting the symmetrical system are not all reduced to the

same extent, but the white and even the black zone may become much broader than usual. In those cases the ground color may be reduced even to the point of complete disappearance. In cases of extreme reduction even the dark zone may be missing, the symmetrical system being represented by white scales only. This particular behavior—that in the reduction of a centric system (symmetrical

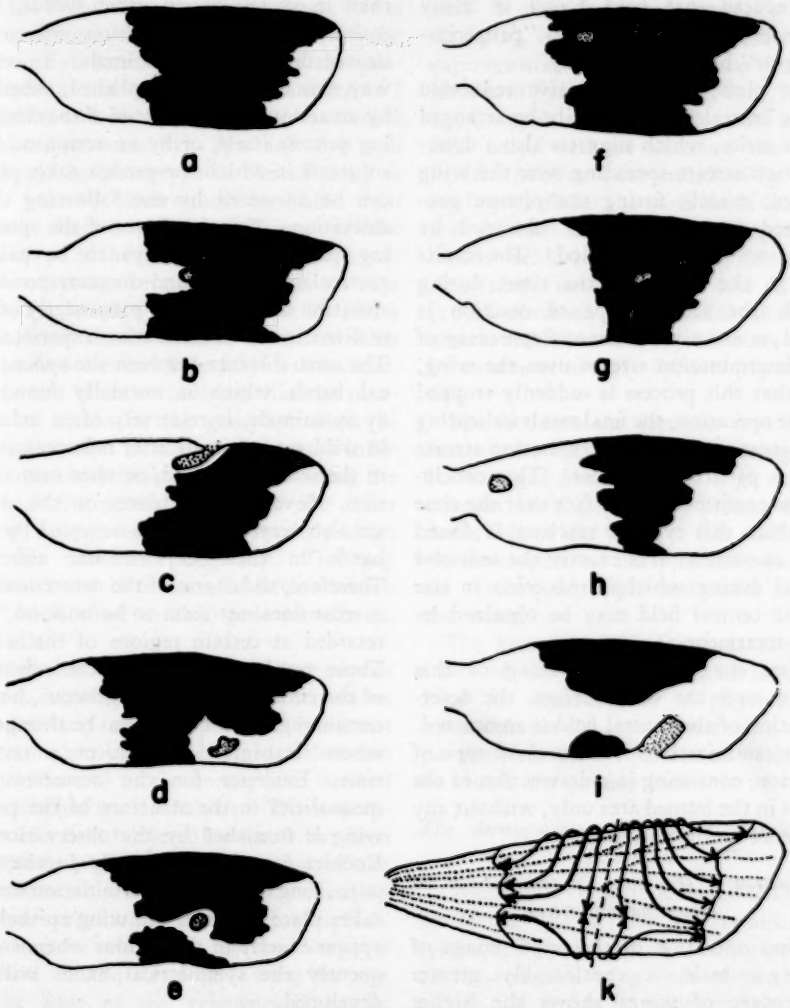


FIG. 8. ALTERATIONS OF THE SYMMETRICAL SYSTEM OF EPHESTIA KUEHNIELLA AFTER CAUTERIZATION

(a) normal. (b–e) after cauterization at the first day after pupation (local reaction). (f–i) after cauterization at the second and third day after pupation (general inhibition of the spreading process). Symmetrical system, black; outer-fields, white. Schematically from Henke (1935) after Kuehn and von Engelhardt. (k) scheme of the spreading process. After Kuehn and von Engelhardt (1933).

system, discal ocellus) the innermost parts disappear entirely before the outer parts are reduced—has been found in many instances and has been called "pauperization rule" by Henke (1933a).

The pictures of progressive reduction of the central field can easily be arranged into a series, which suggests also a determination stream spreading over the wing surface, exactly fitting the picture constructed from the results obtained by operations in the first period. The results lead to the idea that the time, during which the second type of reaction is found, is exactly the time of spreading of the determination stream over the wing, and that this process is suddenly stopped by the operation, the final result indicating the situation of the determination stream in this particular moment. This conclusion is confirmed by the fact that the time in which this type of reaction is found after cauterization is exactly the sensitive period during which a reduction in size of the central field may be obtained by heat treatment.

After the time of spreading of this stream over the wing surface, the determination of the central field is completed. Later cauterizations led to a third type of reaction, consisting in a destruction of the scales in the burned area only, without any influence on the pattern.

### *The action of the genes Sy and Syb on the determination process*

After operation of the pupal wings of Sy sy-animals, a considerably greater percentage of wings shows the higher degrees of reduction of the central field than after operation of wild type (sy sy) moths. This result throws some light on the action of the gene Sy. A certain stage of the spreading process will be more likely to be hit by the operation the longer it lasts. Therefore, the stages determining a very small central field are retained a longer time in Sy sy-animals than in sy sy, or, in other words, the course of the determination stream is slowed down in Sy sy-animals. In what way this effect is accomplished, whether by an action on the impetus of the streaming process itself, or by an action on the substrate in which the process takes place can be answered by the following consideration. Certain phases of the spreading process seem always to be passed particularly slowly, and the corresponding situation of the bands is particularly often realized in the cauterization experiments. The same distance between the symmetrical bands which is normally found in Sy sy-animals, is relatively often induced in wild type animals after heat treatment in the sensitive period, or after cauterization. Several other places on the wing are also very likely to be occupied by the bands in these experimental animals. Therefore, the course of the determination current does not seem to be uniform, but retarded at certain regions of the wing. Those results suggest that the substrate of the current is not homogeneous, but at certain regions there seem to be thresholds whose transgression requires a certain time. Evidence for the occurrence of inequalities in the structure of the pupal wing is furnished by the observation of Koehler (1932) that already in the prepupa, long before the determination stream takes place, folds in the wing epithelium appear exactly in the regions where subsequently the symmetrical bands will be developed.

In the operations on Sy sy wings, certain phases of the beginning of the determination stream are very often encountered. It seems, therefore, that the gene Sy causes a retardation of the determination current by some action on the inequalities of the substrate.

Whether the gene Syb acts on the impetus of the current or on the resistance of the substrate, is not yet known. It is noteworthy, that the inheritance of the factor Syb forms an instance of the phenomenon of "maternal inheritance" (Kuehn and Henke, 1936). In reciprocal crosses between Syb Syb and Syb syb moths, the phenotype of the offspring is not entirely determined by their own genes, but a certain influence of the genotype of the mother has been observed: the offspring originating from a cross Syb Syb mother × Syb syb father has a broadened central field as compared with animals descended from a Syb syb mother. This fact tends to indicate that the manner of action of the gene Syb must be complicated. In some way it must influence the determination process causing the size of the central field. On the other hand, it may act at such an early stage as the unreduced egg cell. The gap between the two times of action which can be ascribed to this gene remains to be filled.

The results of the cauterizing experiments, combined with the observations in genetical and temperature treatment experiments, give a physiological meaning to several of the conceptions derived by morphological analysis. The conception of a field bordered by bands has been established to be due, in the case of the symmetrical system, to a determination stream spreading over the wing surface. The region where the current stops is marked in the developed wing by the white zone of the symmetrical bands. The innermost dark line is a differentiation of the central field; the outermost dark zone, of the outer field. The area, over which the determination stream has passed becomes distinguished from the outside areas, as shown in many instances (e.g., in *P. cynthia*) by a difference of coloration. But even in cases where this difference between central field and outer-field is not developed normally (e.g., *Ephestia*), it can be shown to exist under experimental conditions. Two genes are known in *Ephestia* (Whiting, 1919; Kuehn, 1937, 1939b) which darken the central field only, without affecting the outer-fields. Another gene described by Whiting (1919) makes the outer-fields (external and internal field) sooty, giving to the central field, however, a lighter coloration than usual. Strohl and Koehler (1934) obtained white scales inside the central field, but not in the outer fields, by treatment of early *Ephestia* pupae with $CO_2$.

The fact that the determination stream reaches the upper side of the wing from the fore and from the hind edge suggests a center for the spreading process on the under side of the wing—a fact confirming the developmental unity of the symmetrical systems on upper and under side of the wing.

The heterogeneities found in the substrate of the spreading process may perhaps be regarded as a physiological equivalent for the areas of the wing where pattern elements are particularly likely to be found, the pattern loci.

### *The determination of pattern elements in P. cynthia*

Comparable conditions have been found by Henke (1933a) for the symmetrical system of *P. cynthia* by means of operations on the imaginal wing buds of late caterpillars. If a cut is made in the wing imaginal bud, the pattern of the adult wing corresponds, to a certain degree, to the results obtained after cauterization of *Ephestia* wings at the first day of the pupal stage. The size of the central field becomes diminished, and the operation scar is always situated outside the

central field, the symmetrical bands forming a sharp boundary of the central system against the operated area as well as against the outer-field. This behavior leads in the hind-wing to a withdrawal of the symmetrical system towards the hind margin of the wing. The connection between the central fields of upper and under side remains always uninterrupted. In the fore-wing, the central field may become divided at its narrowest place, giving rise to two symmetrical systems at the hind and fore edge of the wing. The pictures obtained in those experiments resemble closely those found in *Ephestia* after cauterization in the region of the anal vein, so that the same explanation of a determination stream originating at the under side of the wing and passing to the upper side around the fore and hind edge can be applied. At the under side of the fore-wing a proximal symmetrical band may appear after operation, which is not developed under normal conditions, the central field reaching the base of the wing in unoperated specimens.

If a part of the symmetrical system is strongly reduced, but not yet completely eliminated, the "pauperization," already mentioned in *Ephestia*, is observed, meaning that the innermost zones of the system disappear first and the outermost white line last in the course of progressive reduction. The outermost pink stripe, which may or may not be lacking independently of the other elements, forms occasionally an exception, indicating its developmental independence from the symmetrical system, like the corresponding outermost dark stripe of the bands of *Ephestia*. The symmetrical bands of *P. cynthia* as well as of *Ephestia* are shown in this way to be combined elements, the outermost zone being a differentiation of the outer-field. The border of the symmetrical system is in both cases constituted by the white line.

A similar analysis of the factors active in development has been undertaken for the discal ocellus of *P. cynthia* in the experiments of Henke. A certain area of epithelium which will afterwards form the ocellus is already determined in the late caterpillar, and after removal of this "anlage" no ocellus is formed. If, however, some of the ocellus-forming material is left, it regulates into an entire ocellus, indicating that its arrangement into different zones is not yet accomplished. This "anlage" recalls an harmonic equipotential system in so far as it is able to form two or even several complete ocelli after being cut into several parts by the operation. In reduced ocelli, the transparent center and the white zone may be lacking leaving only a yellow spot, conforming to the pauperization rule. The black line bordering only the foremost half of the ocellus, although belonging to the ocellus in its shape, resembles much more the black symmetrical band in its coloration behavior, as already mentioned above. The ocellus therefore can be regarded as another instance of a combined pattern element.

For the pattern elements apart from the central system a similar determination by a spreading process has been assumed, because of the morphological observation that all of them can be conceived as fields or as field border differentiations. No experimental evidence for this view is, however, available. For the ocellus, a similar kind of determination seems likely because of several similarities between ocellus and central system (e.g., concentric arrangement and "pauperization").

Other similarities suggesting also a similar origin have been observed in the behavior of the central shadow. The part of the central field distal to the central

shadow is sometimes distinguished in coloration from the proximal part, a case found in several Saturnid species and also in *Ephestia* under the influence of a gene df (Kuehn and Henke, 1935). Furthermore, in *Abraxas* the row of dark spots representing the central shadow changes its position in the central field after heat treatment at a certain sensitive period (Kuehn and von Engelhardt, 1936). Both observations support the view that the central shadow is a border differentiation between two differing fields, and the similarities of these facts to the well-known behavior of the symmetrical system makes a similar origin not unlikely.

### *Mitosis pattern*

After the sensitive periods have passed, the determination of the wing pattern is completed. Subsequent treatment of the wing by operations, by temperature shocks, or by chemicals leads to abnormalities in scale structure and color production, but not to changes in the distribution of differently colored areas in the wing; that is in the general color pattern.

The first visible effect of the determination process is a peculiar distribution of cell divisions in the wing epithelium at a time immediately following the determination stream (Koehler, 1932; Braun, 1936). At this time, two waves of mitoses pass over the wing from the base towards the margin. In the histological description of the scale formation in *Ephestia* (Koehler, 1932; Stossberg, 1937), it has been shown that before the outgrowth of the scales, every scale-forming cell undergoes two differential mitoses. The same has been shown for *Rhopalocera* by Sueffert (1937). The first of the mitosis waves passing over the wing involves divisions of common hypodermis cells and the first differential divisions of the scale-forming cells. The second wave is constituted of second differential divisions of scale-forming cells only (Braun, 1936). Koehler as well as Braun observed that those cell divisions are particularly frequent in the areas which later on will develop into dark pattern elements. The phenomenon has therefore been called "mitosis pattern." Both waves show maximal mitosis frequencies in the subsequently dark areas, resulting in a greater number of smaller cells per unit wing surface in the later dark areas and accordingly in a higher number of scales in the dark areas in the complete wing. That this mitosis pattern is a direct effect of the determination process has been proved by Braun (1936), who found the areas of maximal cell divisions shifted, according to the subsequently accomplished pattern, after heat treatment in the sensitive period and in presence of the gene Sy. Heat treatment in the sensitive period, besides shifting the mitosis pattern, arrests mitoses up to 24 hours, while cells already dividing finish their mitoses more slowly (Braun, 1939).

### *Histological differentiation of scales of different type*

After this period of the cell divisions, the outgrowth of the scales begins, which has been described by Koehler (1932), Stossberg (1937), and Sueffert (1937). No differences in the behavior of the later differently colored and shaped scales could be found by histological methods (see also Koehler and Feldotto, 1937). However, Braun (1939) proved by the iodine-zinc chloride method of Schulze and by the difference in the time necessary for dissolving the scales by concentrated $H_2SO_4$, that the parts of the wing which later are lighter in color, are at a certain period of differentiation already more chitinized than the subsequently dark areas. This fact accounts for the "relief stage," first detected and interpreted by Goldschmidt

(1920) in several species of butterflies and moths and lately found by Braun (1939) in *Ephestia*. If the still unpigmented pupal wing is removed from its sheath and dried, the subsequently dark scales, owing to their lesser chitinization, collapse, whereas the more chitinized later white scales remain inflated, showing a negative of the pattern in relief. Goldschmidt, interpreting this fact as due to different developmental velocities of the different kinds of scales, accounts for the different pigmentation by assuming that chromogens are present in the hemolymph at certain distinct times only, and that they can enter only the scales not yet entirely chitinized at this time. By showing that in the relief stage and even a considerable time before its appearance, only the less chitinized, i.e. the subsequent dark scales, give a pigmentation when treated with tyrosine, Braun (1939) gave strong support to this view. Goldschmidt (1938) tried also to connect the occurrence of the relief stage with the preceding mitosis pattern, in pointing out that the later dark areas undergo cell divisions at a time when the other wing cells have already undergone all their cell divisions, and that they can therefore be regarded as delayed in development.

The effect of the determination does not only consist in a different pigmentation, but also in a different shape of the scales in different areas. As Kuehn and Henke (1932) have shown, a certain pigmentation in the scales of *Ephestia* is always accompanied by a certain typical shape and structure, the dark scales being always higher and more slender than the white ones. If a change in the intensity or the size of a pattern element occurs under experimental conditions, the shape of the scales is changed according to their pigmentation. The determination, therefore, does not only account for differences in pigmentation, but also in structure of the scales. The problem in this way becomes a morphogenetic one. This is particularly evident in the case of the blue iridescent scales often found in Lepidoptera. Their color, as Sueffert (1929) has shown, is an optical color, caused by the interference of light waves with especially arranged internal chitinous structures.

During the period of scale differentiation, changes in the structure of the scales are induced by heat treatment. At the beginning of this time, a sensitive period for loss of scales has been found by Feldotto (1933) in *Ephestia*, and by Koehler and Feldotto (1935, 1937) in *Vanessa urticae*. Later on, the latter authors found a sensitive period for a change in the shape and structure of the scales, without changes in their pigmentation. Shape and size of the scales may also be altered by starvation in the larval period (Koehler, 1940b).

Shortly before hatching, the pigmentation of the scales takes place. Different colors appear first at different times (Goldschmidt, 1923; Henke, 1933a). In the dark pattern elements of *Ephestia*, the pigmentation process appears to proceed from the base of the wing towards the distal edge (Koehler, 1932), like the mitosis pattern and the chitinization of the scales.

The different time of appearance of the different pigments leads to a peculiar behavior of the wing color of *P. cynthia* in the case of interference between different systems. In cases of reduction of the central field after operation, the ocellus often breaks partly through the symmetrical bands, so that certain areas of the wing are situated in the ocellus as well as in the band. The question is which kind of coloration shall prevail in those areas, the coloration belonging to the ocellus or to the band? Actually the

scales assume that one of the two possible colorations that is first formed in development, notwithstanding for which of the two systems it is characteristic (Henke, 1933a).

### *Inhibition of the development of determined pattern elements*

Immediately before the pigment appears in the wing, a sensitive period for pigmentation occurs. By heat treatment during this sensitive period, only the pigment content of the scales is changed, without any corresponding change in the shape of the scales (Feldotto, 1933; Koehler and Feldotto, 1935). In the sensitive periods of Lepidoptera, therefore, three larger parts can be distinguished. After treatment in the first part of the pupal life, the determination of the pattern and the size of the systems constituting the pattern is changed. In the second part, the forming and the differentiation of the scales is influenced, while in the third part, only the pigmentation can be affected.

A certain number of genes have been described in *Ephestia* that influence the shape and size of the single scales (von Finck, 1938), the distribution of the pigments in the single scales (Kuehn and Henke, 1932), and the color of the scales (Kuehn and Henke, 1929). The mutation b (Whiting 1919; Kuehn and Henke, 1929) causes all light pattern scales which are relatively broad in shape to be replaced by the characteristic slender dark pigmented pattern scales, except for the white parts of the symmetrical bands and of the central spot. In dz dz-animals (Kuehn 1939b) a similar replacement of light pattern scales by dark pattern scales takes place, but in this case it is restricted to the central field. A mutation "he" causes in homozygous condition a weaker pigmentation in all scales of the wing. In producing this effect, an alteration of the chitinization process may play a rôle (Kuehn, 1937, 1939a). The phenotypes caused by the genes he and b have been found to develop autonomously, if grafts of larval skin were transplanted into the fat body of wild type animals (Kuehn and Piepho, 1940). Genes influencing the pigmentation of the scales have also been found in numerous other species of Lepidoptera (see review by Ford, 1937).

A certain boundary is set to the effectiveness of the morphological pattern analysis by the fact that elements which are determined by or at least belong to the potentialities of a certain species, may not become actually developed. In this case experiment sometimes does show the existence of a normally lacking element. Several instances of this kind which seem to be caused by different mechanisms have been described.

No pattern is visible on the under side of the fore-wing of *Ephestia*. It seems, however, likely that it has been determined, as an origin of the determination stream at the under side of the wing is suggested by the direction of its flow, and as the mitosis pattern has been found on the under side of the wing by Koehler (1932). Close inspection reveals that the dark and white scales, which form the pattern elements, are not developed on the under side. It is covered with "ground scales" only, a type of scale which is present on the upper side also, forming the underground and not reaching the surface, so that they do not contribute to the pattern (Kuehn and Henke, 1932). A few pattern scales are, however, present at the tip of the under side and here they actually are arranged so as to form the beginning of the distal symmetrical band.

Another instance of an apparent absence of determined pattern elements is found in the mutation b (black, Whiting, 1919;

Kuehn and Henke, 1929) in *Ephestia*. In homozygous *bb* animals, all scales, except the white ones belonging to the symmetrical bands and to the central spots, are replaced by black pattern scales, so that the dark pattern elements cannot be distinguished. However, the presence of the dark central spots can be shown by the interaction of the gene *s* (Whiting, 1919) which lightens the central field, showing clearly the central spots, or by treatment of bb wings with ultraviolet light at a certain period (Strohl and Koehler). Under the latter influence, light scales are developed in the irradiated area, and the dark central spots appear clearly in the lighter surroundings. The fact that in bb animals the dark pattern elements are present and only covered by the general black pigmentation, has already been seen by Koehler (1932) in observing the course of pigmentation in black animals. In the pupal wing, the pigmentation begins at the normal time in the normal manner, the dark pattern elements becoming colored against a lighter background. Afterwards a stream of black pigment spreads from the base of the wing to the edge, coloring the background dark, so that the pattern elements cannot be distinguished. It is noteworthy that, in this case, the dark scales of the background show the same morphological type as the dark scales in the pattern elements, so that the same coloration is accompanied by the same structure of the scales, but not by the same time of pigmentation.

On the other side, a pattern element may not be visible because it is covered by another one. This case seems to be present relatively often, due to the occurrence of identical pattern loci for different elements. This possibility has already been described for the internal shadow of *P. cynthia*, which becomes visible when the proximal symmetrical band is removed.

Another possibility has been described by Koehler and Feldotto in their modification experiments with *V. urticae* and *V. io* (1935). In these animals, certain elements may become so reduced after heat treatment at a certain time of their sensitive period that they are entirely lacking. The opposite has also been observed—the appearance *de novo* of pattern elements after treatment at the time in which a heat shock has the maximum effect on this pattern system. The central field of *V. urticae* is represented by two large black spots at the fore and hind parts of the wing. After heat treatment at the maximum of their sensitive period, the two spots can become united by a line of black scales, the central field forming in this way a dark band across the whole wing. In the closely related species *V. io* the corresponding system consists of one dark spot at the fore part of the wing only. After a heat shock applied to animals of this species at the time of maximum effect of the sensitive period for the central field, a dark spot in the hind part of the wing appears, corresponding to the hind spot normally present in *V. urticae*. Its behavior resembles that of the foremost part of the central field so much that no doubt exists as to its belonging to the same system.

All these facts show clearly that the developmental possibilities of a certain species of Lepidoptera may be much larger than the pattern ultimately developed, and that different factors during development may be able to abolish their expression. The last case is very interesting in so far as here the suppression of a pattern element seems to be due to the nature of the determination process under natural conditions. The potential pattern element can appear only if the deter-

mination process is raised to a higher level by external influences.

*Rhythmical patterns*

Hitherto, only pattern elements have been dealt with that can be regarded as field structures or field border differentiations. Actually systems of this kind represent the majority of the elements forming the Lepidopteran wing pattern, but they are not the only kind. Sueffert (1927, 1929) has described a certain kind of rhythmically repeated elements (small lines or dots) under the name "purling patterns." Henke (1936) distinguished two kinds of rhythmical patterns: spreading rhythms, characterized by an obvious arrangement around a virtual center, and simultaneous rhythms. Henke is inclined to regard the first kind as caused by a chemical arrangement process like the *Liesegang* phenomenon, the concentric arrangement of precipitates in a colloidal medium, if one reagent diffuses through it from a center, the other one being dissolved in the colloid. The simultaneous rhythms may perhaps be regarded as caused by growth rhythms.

No experimental material is thus far available to confirm these views. Koehler and Feldotto (1935) found a distinct heat sensitive period for the rhythmical elements on the under side of the wing of *V. urticae*. Even on the upper side, where no rhythmical pattern is developed normally, rhythmical elements may appear after heat treatment at the time of maximum effect of their sensitive period. The occurrence of a sensitive period suggests perhaps an origin not too different from the origin of the field patterns.

*Dependent patterns*

Finally, Sueffert described a type of "dependent elements," i.e. elements which show a clear morphological dependence upon the structure of the wing, the veins, and the margin. The most conspicuous instance of this kind of pattern is colorations of the veins. However, most of the other elements show a certain dependence upon the wing structure too, as, e.g., the discal elements, dependent in situation upon the transverse discal vein; the marginal spots in *Ephestia*, situated always at the margin between the veins; and the symmetrical bands of *Ephestia*, which are broader on the veins than between them, assuming an arrow-like shape on every vein.

An experimental analysis of a dependent behavior has been possible for the pseudo-marginal spots on the hind-wing of *P. cynthia* (Henke, 1933a). They represent a row of spots running parallel to the edge of the wing, situated in a proximal direction from the border line, always between the veins (cf. Fig. 1). This relation remains true even under experimental conditions. If a vein is shortened after an operation at the wing imaginal bud, the corresponding spots unite to form a single spot. If new veins are formed the spot crossed by it divides into two. These observations would fit the conception of a direct dependence of the marginal spots upon the veins. If, however, a vein does not reach the margin of the wing entirely, but ends near it, the nearest marginal spot extends in the direction towards the vein (Fig. 9), occasionally even so far that the vein may enter the spot without dividing it. Close inspection of the surrounding area solves this apparent contradiction. The pseudo-marginal spots are situated in a light colored area, the border-field, which is sharply distinguished in coloration from the external field and by a line from the marginal field. The boundary between border-field and external outer-field in normal individuals is slightly bent on the veins in the direction towards the

wing margin. If, however, the vein is shortened under experimental conditions, this boundary follows the vein, forming evaginations in its direction. The marginal spots always maintain a constant distance from this boundary, whether it is bent in a proximal or in a distal direction. This behavior explains the evaginations of the spots under experimental conditions, but not their division by the veins in normal cases. They could be bent in a distal direction like the field boundary and maintain their connection. Therefore, a second factor, the maintenance of a constant distance from the borderline or from the margin is to be assumed. In this way, the pseudosubmarginal spots appear as differentiations of the border-field, which tend to maintain a constant distance from the proximal and distal boundary of this field. The division of the marginal spots is not due to a direct influence of the veins on the spots, but an indirect one, primarily acting on the shape of the field producing the spots.

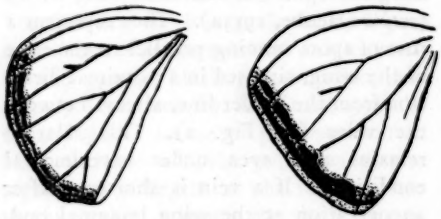

FIG. 9. ALTERATIONS OF THE VEINS AND OF THE SUBMARGINAL PATTERN ELEMENTS AFTER OPERATION OF THE IMAGINAL BUD OF THE HIND WING OF PHILOSAMIA CYNTHIA

After Henke 1933a.

Koehler (1940b) described the occurrence of supernumerary cubitus veins in *Ephestia*. If such a supernumerary vein reaches the margin of the wing, two marginal spots are formed instead of one as in normal animals. If, however, the supernumerary branch unites with its neighbor before reaching the margin, only the normal marginal spot is present. Koehler suggests that the position of the marginal spots may be determined by the situation of the underlying blood lacunae, which determine on the other hand also the course of the outgrowing tracheae.

## CONCLUSIONS

The analysis of the development of the wing pattern of Lepidoptera is far from being completed. We know about the determination of at least one pattern system, the central symmetrical system, by a spreading process in the wing epithelium. But how this process causes its first morphological effect, the arrangement of mitotic figures according to the later developed pattern, is still unknown. Also the gap between this mitosis pattern and the formation of the final pattern consisting of differently shaped and colored scales remains to be filled. In a general way it can, however, be claimed that some of the chief principles of pattern determination have been established. The investigation started with a morphological analysis of the pattern variability in different groups and succeeded in describing and connecting them with the aid of relatively few conceptions, among which the conception of pattern systems and pattern loci are outstanding. Experimental analysis has given evidence for the physiological processes underlying these conceptions. The systems consist of different pattern elements which are caused by the same developmental process and, therefore, react in the same way to external (temperature) and internal (genes) influences. In the best analyzed case, this developmental process is a determination stream spreading over the wing surface. Also in most of the other cases it is best regarded as the formation of fields and field border differentiations. The conception of pattern loci may find its

developmental equivalent in the observed heterogeneities in the wing epithelium which form areas of higher and lower resistance for the flow of the determination current. With the aid of these experimental facts, the morphological analysis is able to give evidence for the developmental processes in wings of species which have not been analyzed experimentally.

On the other hand, the analysis has furnished major contributions to fundamental problems of general biology, mainly the question of gene action. A great number of genes influencing different aspects of pattern formation have been studied and light has been thrown on their influence on the developmental processes, the steps where they exert their action and their interaction with external influences, chiefly temperature alterations. Besides this, a suitable material has been found for the study of several developmental phenomena, as, e.g., the collaboration of parts of different origin in the formation of a single morphological trait.

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# THE LABORATORY POPULATION AS A TEST OF A COMPREHENSIVE ECOLOGICAL SYSTEM

By THOMAS PARK

*Hull Zoölogical Laboratory, The University of Chicago*

*and*

*The Marine Biological Laboratory, Woods Hole, Massachusetts*

## INTRODUCTION

THE time is ripe for a careful and critical scrutiny of certain aspects of the terminology issue in ecology. If judiciously done such scrutiny should furnish an over-view of basic ecological concepts and principles. However, this is not a simple task. It would be easy to hold that all ecological terminology is bad; that the field is not yet ready for a nomenclature of its own; that such a nomenclature can never be of value. It would be equally easy to hold that the ecologists have been unusually perspicacious in matters of terminology and that ecologic terms are both meaningful and empirical. Unfortunately, neither position appears to be sound. It must be granted immediately that any system of ecological terminology that is brief, skeletal yet general is much to be desired. It is apparent that, even if capable of development, such a system is yet to be discovered. There are good reasons for this. The primary ones seem to be (a) that the environmental relationships of organisms in nature are innately complex, and (b) that the evidence necessary to delineate these relationships is sadly lacking.

The present treatment is in no sense a discourse on esoteric terminology. In fact that is a subject about which the author is both skeptical and critical (Park, 1939a). However, I have been interested for over a decade in problems concerned with the experimental and statistical biology of populations and have seen the growth of a good deal of respectable information collected primarily by using insects and microörganisms as experimental material. (For key references see Allee, 1931; Bodenheimer, 1938; Gause, 1934; Park, 1939; Pearl, 1925; Thompson, 1939; and Wright, 1931.) It seems to me that much of this subject matter is ecological in character. This lends impetus to the present paper in which an attempt will be made to apply certain facts and concepts gleaned from population research to a general ecologic system intended to fit a diverse series of natural field communities.

Although the laboratory population studies have been approached from several points of view they share, in the main, certain common properties. Some of these properties may be listed as follows:

(1) There is an attempt in all these studies to express the results in *quantitative* terms. This is a desirable, though not always possible, end-product in any ecological venture.

(2) There is essentially a complete absence of terminology in the studies. This may mean that the results are not too well integrated. It may also mean that this phase of ecology is free from the bias of prematurely coined terms and, by that token, poorly crystallized concepts.

(3) Most of the studies are concerned with important biological variables. Particularly well studied are (a) the factors contributing to population growth—fecundity, fertility, fission rate, success and rate of development; (b) the factors contributing to population decline—differential morbidity and mortality; and (c) the factors concerned with selection pressure. All these factors usually have been analyzed in the presence of differential population densities.

(4) There are certain theoretical generalizations that have grown out of, or along with, these studies. Some of these are far from polished; others are quite well established. For example, Pearl and Reed (1920) have shown that most populations follow a sigmoid curve of growth that they designate "logistic." A criticism of their ideas appears in a paper by Wilson and Puffer (1933). Volterra (1926), Lotka (1934), Nicholson (1933), Nicholson and Bailey (1935), Stanley (1932, 1932a), Thompson (1939), and others have emphasized the mathematics of competition and biotic interactions. Wright (1931), Haldane (1932), and Fisher (1930) have shown in statistical terms the necessity of treating problems of evolution as a phase of the biology of populations and thus have played the important rôle of merging certain aspects of genetics and ecology under a common biological denominator. Dobzhansky (1937) has applied some of these findings to field populations of *Drosophila pseudoöbscura*. Allee (1931, 1940) has delineated the principle of aconscious cooperation to be discussed later and Emerson (1939) and Gerard (1940) have examined once more the population as a supra-organism. Bodenheimer (1938) and Gause (1934) have applied certain theoretical concepts to laboratory data. Hjort (1938) has viewed the population problem in terms of human values.

There appeared recently (1939) a book by Clements and Shelford entitled *Bio-Ecology*. This book has been the subject of much controversy among biologists. One finds among its reviewers (for examples, see Elton, 1940; Hutchinson, 1940) various opinions of its worth ranging from outspoken criticism to moderated praise. The criticisms take the form that the book is unscientific, lacks evidence to back up its concepts, is neither closely written nor well thought out, and is replete with meaningless terms. The praise takes the form that the book has important basic ideas, that it has been written by investigators familiar with a wealth of field material and that it represents a type of synthesis towards which ecology can move with profit.

It is my feeling that it will prove stimulating to select carefully certain of the basic concepts described in the Clements-Shelford book, discuss these concepts in abstract terms and then try to fit them with some of the data that have emerged from laboratory population studies. I think this will be instructive in several ways. First, it will provide a test for seeing if there are close parallels between a natural and an experimental population. Second, it may illuminate the workings of a complex field community since the laboratory populations provide a highly simplified yet complete biological system. Third, such an application will tend towards quantification of ecological phenomena since, in their final form, the laboratory studies are usually expressed in numerical terms. Fourth, there may be an opportunity to examine critically and realistically the meaning, or lack of meaning, of an ecological term when applied to a specific and fairly well analyzed example. It must be emphasized at once that the present article is not intended to pass judgment one way or another on the general

worth of the Clements-Shelford book. That would be presumptious; in fact, there are many aspects of the book I shall not touch on. It *is* the hope that this paper will test some of the issues raised above and aid in clarifying the *modus operandi* of two types of biological associations—the natural community and the laboratory population. This paper will develop as follows: (1) a selection and definition of the important integrative concepts proposed by Clements and Shelford; (2) illustration of these concepts wherever possible using examples taken from the experimental population literature; and (3) a synthesis and discussion of the results. There will be no new terms introduced. From a certain point of view this may be considered a weakness in the paper. The reader may feel with justification that, after spending so much time on the Clements-Shelford system and critically evaluating it, the author should propose and develop a modification that he considers better. I agree heartily that that should be done but personally prefer to wait until ecologists have thought longer and more soundly about the matter. Undoubtedly, at a somewhat later data, someone will prepare such a synthesis. The experimental examples used in this paper will draw on work carried out primarily with the flour beetle, *Tribolium confusum*, and the fruit fly, *Drosophila melanogaster*. Other insect studies will be mentioned briefly where pertinent. The emphasis is placed on *Tribolium* and *Drosophila* because these species have been used extensively in population research and because the author is most familiar with them.

## THE GENERAL BACKGROUND

In their book, Clements and Shelford introduce the reader to a series of ideas and working concepts that are really categories into which, in their opinion, the operational activities of all communities fall. One says "all communities" advisedly for it is maintained by the authors that these activities are similar processes whether found at work in a grassland, a freshwater community, or a marine pelagic community. The processes may and do vary in expression and importance from area to area but, nevertheless, are identifiable and operative wherever a natural grouping of organisms occurs. Obviously then these are the factors we wish to examine in this paper. In the present section these factors will be formalized and illustrated briefly; in the next section they will be related to experimental population studies. At the moment we shall consider the following viewpoints or factors: (1) the philosophical basis; namely, a climax community is a complex social organism; (2) the meaning of habitat; (3) the operational factors, action and reaction; and (4) the significance of aggregation when broken down into its component coactions, co-operation, disoperation, and competition.

### *The community as a social organism*

Clements and Shelford adopt the view throughout their book that plants and animals are associated in natural units over the earth and in the water. These units, designated "biomes," are definable geographically, morphologically (stressing the fact that both animals and plants are integral components), operationally, and developmentally. The existence of such units has led the authors, along with many others, to the conclusion that the community, ". . . is more than the sum of its parts, that it is indeed an organism of a new order. . . ." It is considered, ". . . to be a complex organism, bearing something of the same relation to the individual plant or animal that each of these does to the one-celled protophyte or protozoan." (P. 21.) In short, the authors feel that

the biome is so real a biological entity that there has been established within it new levels of organization and integration that are lacking in the constituent parts. This idea need not be pursued now. We shall return to it later. Suffice it to say that the following positions among biologists seem to be recognizable at the moment: (a) that the concept is real and actually useful in the analysis of biological associations (Wheeler, 1913, 1923; Child, 1924; Emerson, 1939, 1939a; Gerard, 1940); (b) that the concept may be real but without pragmatic importance; and (c) that the concept is a product of loose-thinking and is genuinely misleading (Bodenheimer, 1938; Gleason, 1939). So far as I can determine, most of the human sociologists consider the idea to be archaic.

### *Habitat*

The word "habitat" is used in a loose sense by most biologists and ecologists to mean simply the place or niche that an animal or plant occupies in nature. Thus the habitat of the wood-roach, *Parcoblatta*, is the forest floor and the under-bark of decaying logs; of the red-winged blackbird, a cattail marsh; and of a malarial parasite, the blood stream of a mammal and the gut and haemocoels of a mosquito. This is a helpful way to use habitat and the word will continue to be so applied. Clements and Shelford, however, restrict the word to include only the total physical and chemical environment of a population. They say,

> ". . . habitat comprises all the physical and chemical factors that operate upon the community. Of these, water, temperature, light and oxygen are of vast importance to both plants and animals, and carbon dioxide to all holophytes and a few chlorophyll-bearing animals. The raw materials for food making by the plants are obviously habitat factors, but food itself is not. . . . As to the solutes themselves, some can be used by the animal directly, while others are available only, or usually, in combination. Substratum and bottom are of much significance for great numbers of aquatic animals, and soil is indispensable to most plants and of no little importance to many land animals." (P. 26–27.)

In this paper then we will view the habitat as a physical-chemical frame-work that supports, either directly or indirectly, the complete biota of its respective community. A single example will make the point. Near the end of the last century Möbias (1877) in a significant paper pointed out certain facts about the distribution and structure of an oyster community (biocoenose) in nature. Under the Clements-Shelford system the habitat of an oyster population would include such factors as the substratum; sea-water, both as a physical medium and a chemical solution, and pressure, light, temperature, salinity, hydrogen ion factors and so on. The habitat would not refer to a particular niche occupied by a single oyster nor would it imply anything about the biotic interactions within the oyster population. In the present paper we shall use habitat in the sense of Clements and Shelford. An interesting philosophical discussion of habitat has been published recently by Haskell (1940).

### *The cycle of action and reaction*

It is apparent on purely logical grounds that if organisms live in a physical habitat such as has just been described there must be certain basic operations continually occurring between these two elements of the environment. Clements and Shelford regard these operations as the *primary* cycle of cause and effect within the community and designate those forces operating as action and reaction. By action is meant the influence impinged on the community or population by the habitat. By reaction is meant the influence impinged on the habitat by the community. Thus if community is represented by "C" and habitat

by "H" the definition can be symbolized as follows:

$$\text{Action} = H \rightarrow C$$
$$\text{Reaction} = H \leftarrow C$$
$$\text{The cycle} = H \rightleftarrows C$$

A brief quotation will help:

"In the plant matrix of the land biotic community, the causal sequence is a fairly simple cycle. The action of the habitat as expressed in stimuli gives rise to responses on the part of the plant or community. These in turn operate on the habitat, producing reactions that modify it, and then again in turn its action on plant life follows" (*Bio-Ecology*, p. 30).

There are some inappropriate implications, however, in using the term "primary" in connection with this cycle. We know that there must be an original relationship between habitat and organism that, in truth, is a primary or *first* action-reaction cycle. But this is not to admit for a moment that later cycles are also primary. In reality they are secondary, tertiary, or higher in character and depend on the development and maturation of earlier action-reactions and coactions that have emerged in the population life-history during the interim. In my opinion, the system of Clements and Shelford does not differentiate too adequately these temporal and structural gradations in the action-reaction cycle. We shall return to the point when discussing the conditioning of flour by *Tribolium* populations.

Action and reaction are so obvious that numerous illustrations will immediately suggest themselves to the reader. The importance of the concept seems to lie in just this comprehensive fact: namely, that these ecological forces are operating irrespective of the type of community under consideration and thus are integrating phenomena common to all biological associations. Organisms in a community must adjust to actions of the habitat. Changes in climate, or substratum, or day to night, or, in a littoral marine community, tide level are all habitat changes that may act on the population and induce an adjustment. We shall examine laboratory illustrations of these actions later. Likewise, reactions are easily noted. An excellent case is the influence of plants and animals on soils. Here, the community reacts on the habitat in one of three general ways: (a) reactions may give rise to new soils or contribute materials that eventually form soil; (b) reactions may protect the soil against, say, erosion, or trampling, or burrowing; and (c) reactions may change the texture, structure, or general character of soil to a noticeable extent (*Bio-Ecology*, p. 72). The importance of such processes need not be pursued.

### *Aggregation and its end effects*

In any biological association there must be more than the primary cycle of action and reaction. Another cycle becomes established that has as its basis the aggregation or grouping of the plants and animals within a particular habitat. This is another way of saying that in a population the inter-individual responses between the members of that population are of great importance. These responses are designated by Clements and Shelford as "coactions." We can visualize and even analyze a single coaction between one organism and another. It is apparent, however, that it is the statistical, or summed aspect of coaction, that is significant as an integrating factor in the community. In the community this coaction is frequently inter-specific as well as intra-specific. Thus we may imagine a terrestrial region where the eating of a certain rabbit by a certain lynx is of no significance ecologically while the predation pressure of the lynx population on the rabbit population may be a coaction of considerable value in shaping the course of the entire community

(see MacLulich, 1937). In this paper then we shall view coaction as arising out of the basic biological response of aggregation. We need not stress here that aggregation in certain cases may be a closely-knit, compact phenomenon or, again, may be merely a diverse, loose-grouping of organisms (see Allee, 1931). Clements and Shelford state,

> "The process of aggregation lies at the basis of social life in the biotic community, and hence it exhibits the most intimate relations with the other functions of the complex organism. It is the very essence of the association of organisms in the dynamic sense, and is primarily concerned with the integration of all the groupings, from the simplest family of plants or animals to the most highly differentiated climax. Like all community functions, it is the collective response of organisms to their environment, and in its turn it produces social patterns of all degrees of complexity" (p. 145).

It is not sufficient to label all biotic interactions as coactions and let the matter stand at that since coaction may have different end-effects on the community. Clements and Shelford have recognized three basic coactions on the basis of their effect on the coacting organisms. These are co-operation, disoperation, and competition. We shall try to differentiate briefly between these and also point out some logical fallacies in them.

### *Co-operation*

In a philosophical sense some degree of co-operation between members of a community must be present in order that such a community can exist. This is a time-honored dictum among biologists. Darwin suggested the point in his writing and, in ecological literature, the idea goes back at least to Forbes (1887). (For a recent discussion of this point see Allee and Park, 1939). It is true that much of the co-operation is scarcely above the level of mutual toleration and equally true that most of it is merely a by-product of certain coactions. In other words, there is co-operation in a community without the development necessarily of complex social processes to produce it. The latter, of course, may also be present in various degrees of development as the cogent syntheses of Allee (1931, 1934, 1938, 1940) have shown. In a population it would appear that many of the disadvantageous effects associated with crowding are balanced and counteracted by the advantageous effects growing out of co-operative coactions. "It is obvious that, while co-operation rests upon mutual tolerance in terms of habits and space, its positive values are derived from the conservation of energy and material, especially food, from division of labor, and from increased care, parental or nutricial." (*Bio-Ecology*, p. 150.) In considering the community as a complex social organism, co-operation becomes very important since it stresses the fact that one set of processes may bolster and implement another. This is analogous to what happens within an individual organism where many physiological processes interdigitate markedly with others. The recognition of synergism by physiologists is a case in point.

However, there are still some questions about the nature of co-operation that are left unanswered in the literature. These questions can be stated stylistically. Consider the coactions existing between two organisms, O and O′. Logically, so far as co-operation is concerned, these coactions can take the following five forms:

(1) O and O′ may both benefit from the association.
(2) O may benefit and the effect on O′ may be indifferent.
(3) O′ may benefit and the effect on O may be indifferent.
(4) O may benefit and the effect on O′ may be deleterious.
(5) O′ may benefit and the effect on O may be deleterious.

There is an element of co-operation in each of the above associations but in all but the first there are also elements of indifference, or disoperation, or competition. For example, in a predator-prey coaction one individual is the winner (predator) and another the loser (prey). Is the effect of the coaction on the predator to be called co-operation? There is need here for someone to examine critically this aspect of the co-operation concept and define it more rigorously than Clements and Shelford have done.

Our concern later will be with pointing our certain coactions in populations and showing that they result in end-effects that are co-operative or advantageous in terms of group success. At the moment we wish to suggest merely the nature of co-operation; to indicate that it arises from certain aggregate coactions within a community, and that it has value in integrating and favoring the development of that community. We wish to point out also a fact frequently neglected by both population students and ecologists: namely, that natural selection can operate on these co-operative coactions and select *as a unit* the population. This means that selection itself frequently emerges as a factor that integrates and shapes the population. Emerson (1939a) has pointed out that selection can operate on either an intraspecific (single species) or an interspecific (mixed species) population. As an example of the latter type he states:

"Cleveland has shown that colony life is essential in the primitive termites because the symbiotic protozoa are lost at each molt and reinfection can only occur through association with non-molting individuals. The mutual adaptive interspecific co-operation of these diverse animal populations can only be explained through the action of natural selection on the interspecific unit. Thus we find population biology merging with community ecology" (p. 296).

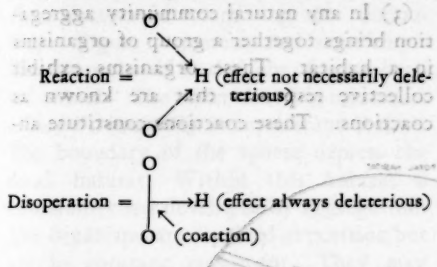
*Disoperation*

The aggregation of organisms within a community results in coactions that are harmful as well as beneficial (i.e. co-operative). Clements and Shelford propose to recognize those coactions that have immediately harmful effects under the term "disoperation." They say,

". . . disoperation stands in direct contrast to co-operation in consequence, but it is less clearly distinguished from competition . . . disoperation includes chiefly those harmful effects that have to do with changed conditions or behavior, as in the accumulation of carbon dioxide, toxins or excreta" (p. 157).

It appears that disoperation must be viewed primarily as a deleterious effect impinged on the habitat; for example, the addition of poisons to the medium. If this is true how does disoperation differ from harmful reaction? This is a point not clearly treated by Clements and Shelford. I think the answer is that in many cases there is no fundamental difference between the two processes. There may be situations in a natural community where the two are distinct but frequently they must merge. Theoretically, a single organism could elaborate some toxic product and add that product to the habitat. This would be a reaction in the strict sense of the word since it does not depend on coaction between organisms. It is also possible that each member of a certain group of organisms within a community could influence its habitat completely independent of the fact that it was associated with like forms. This would also be a reaction system. However, in a typical community an important increment of the total effect would result from coactions that produce such a toxic product in considerable quantity. This would be disoperation. Possibly, there is some practical distinction between reaction and disoperation on the basis of the *rate* at which

the habitat is modified. Here, the rate might be directly proportional to the population density and thus be a function of coaction. The process of disoperation may be symbolized and contrasted with reaction by letting "H" stand for habitat and "O" for organism as follows:




Several examples of disoperation given by Clements and Shelford may be mentioned. A common disoperation among plants occurs in forests where carbon dioxide and acids are added to the soil by the population. These substances act as a barrier to invasion by certain species and may even eliminate some forms already present. They may, in other cases, permit other species to get established. Also in forests, leaves may accumulate on the floor and prevent germination of new plants. In animals, crowding frequently brings about disoperation by adding toxic excreta to the habitat. We shall make an attempt later to delineate disoperation more closely but in no case shall we urge that this factor is always recognizable in any discrete sense in the community.

## COMPETITION

The last factor to be considered is competition. This, like co-operation and disoperation, also arises as a natural consequence of aggregation and is based on coaction. Clements and Shelford view competition as ". . . a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms" (p. 159). They also state, ". . . the essence of competition is the attempt to secure more than a proportionate share of a limited supply of something, e.g., raw materials, food, space or material for construction" (p. 157). Competition is usually most severe between organisms that have similar environmental requirements. It is not, however, limited to intra-specific coaction. There may be all degrees of competition ending in situations in communities where plants and animals are competing with each other. We shall view competition in a statistical sense as a population pressure resulting from the demand made by many organisms on a limited supply of raw material. This seems worthy of emphasis. The time is now past for thinking of competitive phenomena mainly in terms of individual battles between two organisms for an item of food, a mate, or a breeding site. Both the ecologist and the geneticist must be ready to view, and more importantly, to *analyze* competition as a selection pressure growing out of coactions that are based on group or population activity. Obviously, there will not be one competition in a community but many and the number will depend on the size and complexity of that respective community. It should also be stressed that the end-results of competition may vary according to the duration of the competitive phenomena. From a short-time viewpoint, competition can be regarded as harmful in its effects since it reduces the supply of energy and material and also decimates certain elements of the population. However, this is not true necessarily over longer periods of time since competition sets up positions of dominance and subordination and thus becomes an essential factor in community integration and succession. Over still longer time spans competition shapes selection pressures and thereby emerges as a

prime force in speciation. An interesting theoretical discussion of competition is presented by Nicholson (1933) who, so far as I can make out, views this coaction primarily in terms of food and feeding pressures. Nicholson's concepts are discussed and criticized by Thompson (1939).

A final question need be asked here: can disoperation, co-operation, and competition be clearly differentiated? The answer is yes in terms of formal definition but no in terms of many actual cases. We shall omit further discussion of this point until later in the paper when we are dealing with experimental material.

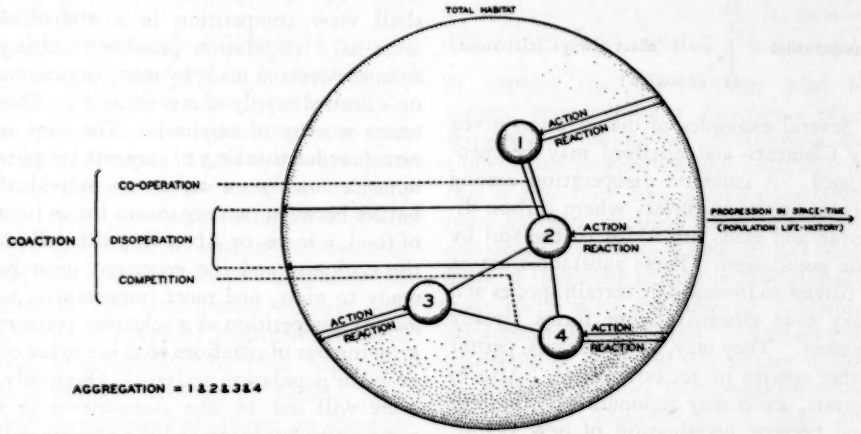



FIG. 1. SCHEMATIC REPRESENTATION OF THE ECOLOGICAL SYSTEM DISCUSSED IN THE TEXT

*Summary*

Before going on a brief summary of the concepts developed by Clements and Shelford is in order. The following points may be made:

(1) The authors adopt the view that the biotic community is a complex social organism. They feel that this view aids in understanding intra-community dynamics.

(2) The habitat is defined as the physical-chemical environment of the community. It has been shown that a primary cycle of cause and effect results from the interplay between habitat and its component population. This cycle is constituted by two operations; (a) action, or the influence of the habitat on the community, and (b) reaction, or the influence of the community on the habitat.

(3) In any natural community aggregation brings together a group of organisms in a habitat. These organisms exhibit collective responses that are known as coactions. These coactions constitute another cycle of cause and effect in the community. Coactions influence the community through (a) co-operation, which has positive value for the co-operating organisms; (b) disoperation, which has deleterious effects on the acting organisms largely through influence on the habitat; and (c) competition, which is an expression of the fact that certain coactions are directed towards exploiting an environment limited in its potentialities.

(4) The integration of a community, that is, its cause and effect relationships, is based on the continuous interoperations of the primary and coaction cycles. These cycles establish the organisms in positions

of dominance and subordination within the community. These positions are not static but are dynamic in character; they are subject to change as the primary and secondary cycles change.

It is possible that an over-simplified diagram may aid in visualizing the rôle of these factors in integrating the community. Figure 1 represents such an attempt. The figure should be thought of as a spherical model. The entire drawing represents a biotic community at any instant of time. The boundary of the sphere depicts the total habitat. Within this habitat a community has developed by aggregation. The organisms are not fixed in position but are in constant movement. They may remain relatively fixed, that is, they exhibit slight movement, for a considerable period of time. This would be the case in most climax communities where biotic balance is well established and the total population maintains essentially an equilibrium. The organisms (balls) are arranged in positions of dominance and subordination. They owe these positions to the interactions of the primary and secondary cycles within the community. The figure shows each organism related to its habitat by action and reaction. It also shows that coaction exists between all members, although all possible coactions are not drawn for the sake of simplicity, and that the coactions may result in cooperation, disoperation, or competition. By moving the model in one direction we get the analogy of change in the community in time and space (ecological succession) with patent modification of habitat and cause and effect cycles.

### *Critique*

A word of evaluation of the Clements-Shelford system is appropriate here. It is obvious that the scheme is over-simplified and that, for many cases, one concept merges so imperceptibly into another that the terms lose objective value. It is also obvious that there is not too much evidence among the data of ecology to test critically this system. One can easily understand the remarks of Hutchinson (1940, p. 267) who, in reviewing *Bio-Ecology*, said,

> The general principles that are supposed to emerge are, however, mainly classificatory; processes occur in different communities that can be placed in a single category and designated by a single term. The general principles of ecology therefore appear as a set of rules for the construction of a language. This may be inevitable in the present state of the science; it is, however, uncertain that the language of *Bio-Ecology* will ever become a universal tongue.

It is also possible to agree with Hutchinson when he points out that the authors neglected the possibilities of statistical treatment when dealing with questions of competition and equilibrium. Despite these obvious objections the Clements-Shelford concepts do aid in classifying ecological phenomena and, more importantly, in arranging these phenomena into something of a working pattern. Doubtless with time a sounder system will be developed but to date this is the best, *in fact the only*, framework of its kind available for the use of ecologists. With this general background we wish to turn our attention now to experimental populations and see if they can be interpolated into the system of Clements and Shelford.

### LABORATORY POPULATION STUDIES

Earlier in the paper it was pointed out that this effort would concern itself largely with studies made on the flour-beetle, *Tribolium confusum*, and the fruit fly, *Drosophila melanogaster*. From time to time, cases using other forms as examples will be cited but attention will center on these two. It should also be remembered that it is not our primary interest to introduce

new facts about insect populations. Rather, the interests lie in organizing and orienting a series of diverse phenomena into an ecological framework; namely, that of Clements and Shelford. Analogically, we are doing what the statistician refers to as "curve fitting." We have a hypothesis—an ecological system—and the facts—the population data—and are interested in seeing how well the two are correlated. An account of the husbandry of *Tribolium* has been published by Park (1934a, 1937a) and Good (1936). Similar material for *Drosophila* has been assembled by Morgan, Sturtevant and Bridges (1925) and Hammond (1938, 1939).

### *Habitat*

*Tribolium confusum.* It is difficult to imagine a more restricted total habitat than that of this species. A bottle or dish containing some sort of pulverized grain is all that is required as far as medium is concerned; the beetles spend their entire life-cycle under such conditions. The important additional factors are temperature, preferably now below 22° or above 32°C. (Chapman and Baird, 1934), and a relative humidity ranging from 25 to 75 per cent in the experimental incubator. Holdaway (1932) has shown that flour reaches a moisture equilibrium with the humidity of the air. In most of the experimental work with *Tribolium* an effort has been made to control as precisely as possible the habitat. Thus, for a certain experiment the following constant conditions usually obtain: (1) control of volume, surface exposure, and kind of medium; (2) control of temperature (frequently maintained at 28°C.); (3) control of relative humidity (humidities of 40 to 50 per cent and 75 per cent have been used most commonly); and (4) control of light by culturing the population in absolutely dark incubators. Oxygen supply and carbon-dioxide accumulation do not seem to be important in the habitat of *Tribolium* since, as far as the experiments to date go, there is no evidence that these operate as limiting factors. The rate of oxygen consumption of male and female imagoes has been determined (Park, 1936) but this is a physiological datum of no immediate ecological significance.

Thus it is apparent that the habitat of *Tribolium* is easily and rather exactly definable in the terms proposed by Clements and Shelford. This habitat is more easily envisaged than that of a beech-maple climax community. The latter is a case where there are more interoperating factors and much more variability. Both, however, are real entities that can be analyzed. There is no difficulty in applying this phase of the habitat concept to laboratory populations of *Tribolium*.

There is one complication. Clements and Shelford state, "The raw materials for food making by the plant are obviously habitat factors, but food itself is not, either for animals or hysterophytes" (p. 26). This does not seem to be true for *Tribolium*. The primary source of the beetles' food is the grain which *is* a major part of the habitat. There are secondary food sources based on coactions such as cannibalism. But these are of relatively slightly nutritional importance in terms of the complete population. Therefore, it will be necessary to include food supply as a habitat factor when dealing with the *Tribolium* studies. I am not sure this really transgresses the definition. In a natural terrestrial community many subterranean forms, as annelid and nematode worms, get their nutriment from organic material dispersed throughout the soil. In this case soil is a habitat factor in much the same way as flour for *Tribolium*. Also, certain termites and the

roach *Cryptocercus*, eat wood directly and obtain starches and sugars by means of the symbiotic activity of intestinal flagellates. In this case a log or a tree is an important part of the habitat. Unless I have misinterpreted Clements and Shelford, it seems possible to retain their concept of habitat and still have it apply in certain cases to food supply. It is now experimentally feasible to split the habitat of *Tribolium* so that the food elements can be separated from inert physical medium and substratum. A recent abstract (Park and Burrows, 1939) called attention to a synthetic medium in which *Tribolium* could be cultured. In this medium a finely powdered wood dust formed the nonnutritive base and certain substances (casein, dextrose, Osborn-Mendel salt mixture, and yeast) added to the wood served as the food supply. This synthetic medium is a habitat in the same sense as grain but it can be broken down chemically more readily than can flour.

*Drosophila melanogaster*. The habitat of *Drosophila* reared under experimental conditions offers certain complications not present for *Tribolium*. The fruit fly is cultured in a more atypical environment than the flour beetle. While the latter genus undoubtedly arose as an under-bark form (Good, 1936) it is largely confined at present to flour and cereal products. Thus a container of flour if large enough is a quite natural habitat for *Tribolium*. *Drosophila melanogaster* probably arose as a tropical and subtropical form correlated in its distribution with fruit. The laboratory habitat of *Drosophila* therefore departs more from a natural habitat than is the case for the beetle. In one sense an analysis of a *Drosophila* habitat is simpler than for *Tribolium*. The former feeds apparently on yeast mycelia (Morgan, Sturtevant and Bridges, 1925; Hammond, 1938–1939) that grow on a nutritive base. This means that the feeding mechanisms of the fly population are coactions similar in principle to those developed for field communities by Clements and Shelford. Here, the habitat can be separated partly from food although *Drosophila* also probably utilize agar medium to some extent as nutriment.

Since most of the population work with *Drosophila melanogaster* has come from the laboratory of Raymond Pearl we shall stress the habitat used by that group. From our viewpoint the total habitat can be broken down into four units: air volume in the container above the medium; the exposed surface of the medium; the medium proper; and the experimental conditions maintained in laboratory incubators. Later it will be shown that all these factors are important, in one way or another, in our ecological system. Suffice it to say here that (1) the medium furnishes a physical substratum in which the larvae burrow and develop; (2) the surface of the medium furnishes a niche for the growth of yeast, feeding of the flies, copulation and associated behavior responses and oviposition; (3) the air volume within the bottle is an area for flight; and (4) the entire bottle can be maintained in an incubator under constant conditions of temperature, humidity, and light. As was the case for *Tribolium*, oxygen deficit and carbon dioxide accumulation normally do not appear to be limiting factors. The medium used (Pearl and Penniman, 1926) is a synthetic composition of agar plus certain salts with the pH regulated. This medium ("S-101") has the virtue of reproducibility and considerable constancy and, while it probably does not yield as large populations as the typical cornmeal-molasses of geneticists, it is easier to standardize and, due to its transparency, it permits fecundity counts to be made.

### *Action*

Action has already been defined and illustrated as the effect of habitat on the community. In this section several examples of action as it occurs in *Tribolium* and *Drosophila* populations will be discussed.

TABLE 1

*Duration of egg, larval and pupal stage of Tribolium confusum at 22°C. and 32°C.*

(Data of Chapman and Baird, 1934.)

| STAGE | TEMPERATURE (centigrade) | MEAN DURATION (days) | COEFFICIENT OF VARIABILITY (per cent) |
|---|---|---|---|
| Egg | 22 | 14.09 ±0.17 | 1.7 |
| | 32 | 4.41 ±0.09 | 3.0 |
| Larval | 22 | 61.10 ±3.27 | 8.0 |
| | 32 | 17.35 ±0.52 | 4.3 |
| Pupal | 22 | 17.86 ±0.59 | 5.2 |
| | 32 | 5.37 ±0.48 | 13.1 |

TABLE 2

*Rate of oviposition of Tribolium confusum females cultured at 22°C. and 32°C. for 13 days*

(Data of Chapman and Baird, 1934.)

| TEMPERATURE | MEAN EGGS PER FEMALE PER DAY | COEFFICIENT OF VARIABILITY (per cent) |
|---|---|---|
| 22 | 1.898* ±0.797 | 62.2 |
| 32 | 10.729 ±1.948 | 26.9 |

* Mean less than 3 times its probable error.

*Tribolium.* Temperature and humidity are two habitat factors that have been worked on for *Tribolium.* Chapman and Baird (1934) kept populations at temperatures of 17°, 27°, and 32°C., and measured the effect of these temperatures on (1) duration of the egg, larval, and pupal stages and (2) rate of oviposition. Their results are summarized in abbreviated form in Tables 1 and 2. These data are straight-forward and, from a physiological viewpoint, commonplace. They show that the rate of metamorphosis is more than tripled by a ten degree rise in temperature and that fecundity performance at 32° is nearly six-fold that at 22°. From the point of view of this paper the data are instructive in that they furnish a diagrammatic example of action: namely that temperature, a habitat factor, acts on a population and increases its rate of development and reproduction. Obviously, these two responses are of the greatest importance in population growth. It is apparent then that temperature must be viewed as a highly significant habitat factor. In most of the studies to be discussed the rôle of temperature will be ruled out. This is an experimental simplification only and does not mean that this factor can be neglected in any complete population analysis of *Tribolium.*

Most action elicits some of its effects on the population through coaction. Temperature is probably as pure an example of uncomplicated action as any case that could be found. A stimulus, temperature, is presented and the population responds in terms of rate effects. These rates are primarily controlled by temperature *per se;* that is, by the specific action of this habitat factor on the physiology of the individuals comprising the population. In the case of most habitat influence the cause and effect cycle is more circuitous as we shall see. Further examples of temperature as a habitat factor for *Tribolium* can be found in the following: Chapman, 1931; Dick, 1937; Good, 1936; Nagel and Shepard, 1934; Oosthuizen, 1935; Park, 1934a, 1935a. A good discussion of temperature coefficients applied to insect oviposition appears in the paper of Harries (1939).

An interesting case of habitat action on *Tribolium* populations is reported by Holdaway (1932). In this investigation beetles were reared under relative humid-

ities of 25, 50 and 75 per cent. It was shown that humidity effects varied with the metamorphic stages. Thus

"... viability of the eggs and pupae is at a maximum at low humidities, while for larvae it is at a minimum. As regards the duration of the various stages there is little effect on eggs and pupae. ... The larval stage is the one in which duration is most affected by atmospheric moisture. It increases with decrease in humidity" (pp. 296–297).

These results are clear-cut illustrations of habitat action. They show that certain beetle stages have their developmental optima at certain humidities. In this respect the data are similar to those actions described for temperature. However, there is a further complication. Holdaway showed that the total population attained its greatest size when cultured at 75 per cent relative humidity. In part this is an expression of an interesting coaction elicited by the action of humidity. Ford (1937, p. 4) summarizes these findings as follows:

"Of particular importance, however, in relation to the size of the balanced population is the eating of eggs and pupae. Holdaway suggests that the feeding stages of *Tribolium*, i.e., larvae and adults, may utilize the non-feeding stages, i.e., eggs and pupae as sources of moisture. This might account for the increase in size of the asymptotic populations with increasing humidity; for at 75 per cent relative humidity the flour itself contains more moisture than at 25 per cent relative humidity, and consequently there is less need for larvae and adults to feed on eggs and pupae, and therefore a greater survival of these stages."

Holdaway himself concludes

"It can then be affirmed that the mechanism by which atmospheric moisture regulates *Tribolium* populations is an alteration in intensity of the normal biotic control which this species can exert on itself; or in other words, the effect of the physical factor humidity, on the insect population is *per medium* of a biotic effect, the intensity of which is regulated by the physical effect of atmospheric moisture on the moisture content of the flour." (P. 298.)

In this connection the paper of Voûte (1938) should be consulted.

From our viewpoint this action system can be summarized as follows: (1) the habitat factor is humidity; (2) humidity has end effects on both the component stages of the population (eggs, larvae, pupae, and imagoes) and the equilibrium point of the total population; and (3) the action of humidity is in some cases direct; that is, a specific humidity effect on the physiology of a certain stage, and indirect in others; that is, operating by altering coaction.

*Drosophila.* Temperature is an important factor for *Drosophila* populations as well as for *Tribolium*. Its action can be illustrated by summarizing briefly some of the effects of temperature changes on oviposition, metamorphosis, longevity, and body size.

*Oviposition.* An interesting analysis of the effect of temperature on fecundity appears in the work of Alpatov (1932). This author wanted to see if the temperature at which *Drosophila melanogaster* was *reared* (i.e. the metamorphic period) would have any effect on the oviposition of the flies as adults. To get at this he cultured one group of fly populations at 18°C., and another group at 30°C. As soon as these flies emerged they were all placed in a constant temperature of 25°C., and their life duration, total egg production, and rate of egg production per day were assayed. Alpatov's data are summarized in abbreviated form in Table 3. This table shows that (1) flies bred at 18° produced more eggs than flies bred at 30° even though the temperature at which the imagoes were kept was the same, 25° in both cases, and (2) the 18° females lived significantly longer than the 30° females. This is a case of a "deferred" habitat action. Temperature acts on the larvae and the effect of this can be detected later in

fecundity performance and longevity. Alpatov thinks that the larvae develop so rapidly at 30° that they emerged in an undernourished condition as imagoes. It is possible that, in addition to the action of temperature in increasing the rate of metamorphosis, food competition between the larvae of the 30° populations is intensified. Again this may be a case where a habitat action is the primary influence with a subsequent coaction the secondary influence.

TABLE 3

*Oviposition of Drosophila females reared at 30°C., and 19°C., and kept as imagoes at 25°C.*

(Data of Alpatov, 1932.)

| TEMPERATURE OF DEVELOPMENT / TEMPERATURE OF IMAGINAL LIFE (degrees C.) | TOTAL NUMBER OF EGGS | EGGS PER DAY | FEMALE DURATION OF LIFE (days) |
|---|---|---|---|
| 30/25 | 430.3 ±33.4 | 14.84 | 31.58 ±1.74 |
| 19/25 | 941.1 ±35.9 | 26.28 | 39.05 ±1.63 |

Another case where temperature has been shown to affect oviposition is reported by Dobzhansky (1935) for *Drosophila pseudoöbscura*. This author described for this species two physiological races, A and B, that appeared alike anatomically but were not interfertile. He found race A was normally an inhabitant of areas where the climate was warm and variable while race B lived in damp, cooler areas. Dobzhansky demonstrated that race A females produced more eggs than race B females when their fecundity was assayed at 25° and 27.5°. However, race B females produced more eggs than A at 9°, 14°, and 19°C. This is an interesting example of the action of an experimental habitat because of its obvious connection with habitat factors obtaining in the field.

*Metamorphosis.* One of the earlier analyses of the action of temperature on the duration of the larval and pupal stages of *Drosophila* was that of Loeb and Northrup (1917). Their data are summarized in Table 4 where it is shown that both larval and pupal development is accelerated by increased temperature within the range reported. These results are quite similar to those summarized already for

TABLE 4

*Duration of life of Drosophila reared asptically in various temperatures*

(Data of Loeb and Northrop, 1917.)

| STAGE | MEAN DURATION OF LIFE (days) | | | | |
|---|---|---|---|---|---|
| | 15°C. | 20°C. | 25°C. | 27.5°C. | 30°C. |
| Larval..... | 17.8 | 7.77 | 5.82 | 4.15 | 4.12 |
| Pupal..... | 13.7 | 6.33 | 4.23 | 3.20 | 3.43 |

*Tribolium* except that in this case the flies were cultured under aseptic conditions free from micro-organism contamination. Another analysis of temperature and metamorphosis is reported by Hammond (1938–1939) in discussing the work of Bonnier (1926).

"Bonnier, using a sex-linked mutant, yellow stock, observed his culture bottles every two hours and removed each pupa formed during the preceding period to a separate bottle and later observed these bottles every two hours while the imagoes were emerging. His results were as follows: high temperature speeded up development in both larval and pupal periods. At 30° the females developed significantly faster than the males in both the larval and the pupal stages. At 25° the pupal period was significantly shorter for the males than for the females (difference 4.1 hours), but there was no significant difference in the larval period." (P. 40).

*Longevity*. There is a good deal of evidence to show that temperature may influence a *Drosophila* population by its action on life duration. This is an important case to include in a discussion of habitat action since the significance of mortality from the population viewpoint hardly can be overstressed. A summary of many such cases is given by Pearl (1928) and some interesting ecological interpretations are suggested by Bodenheimer (1938). A specific illustration is in order. Alpatov and Pearl (1929) reared flies at 18° and 28°C., and as the flies emerged they were placed in populations maintained at 18°, 25°, and 28°. Thus there were two temperature series during post-embryonic development and three series during imaginal life. The data are summarized in Table 5 where it is shown that flies that had metamorphosed at 18° always lived longer, as a population, than flies reared at 28°. This is true for both males and females although the latter are more longevous in all series. The authors interpret their results as follows:

TABLE 5

*Effect of temperature of metamorphic period and imaginal period on life-duration of Drosophila*

(Data of Alpatov and Pearl, 1929.)

| TEMPERATURE DURING IMAGINAL LIFE (*centigrade*) | PERCENTAGE WHICH DIFFERENCE BETWEEN FLIES REARED AT 18°C. AND 25°C. IS OF 18° FLIES | |
|---|---|---|
| | Males | Females |
| 18° | 19.5 | 7.6 |
| 25° | 16.1 | 12.7 |
| 28° | — | 7.0 |
| Mean | 17.8 | 10.2 |

"... the effect of increased temperature is to speed up the *rate* of the biological processes involved. In the 18°C. flies we have a *slow rate* of energy expenditure in growth and during imaginal life (flies very inactive), and we should therefore expect ... the lengthened duration of imaginal life which we observe. In the 28°C. flies there is a short developmental period and a consequent *rapid rate* of energy expenditure during growth and during imaginal life (flies very active). This leads to the expectation of a short duration of imaginal life, which is in fact observed." (P. 65.)

This is another case where the habitat factor, temperature, plays its primary rôle by altering certain physiological velocities associated with mortality.

*Body size (imagoes)*. The final habitat action we shall discuss here is the influence of temperature on body size. In the study just reported (Alpatov and Pearl, 1929) the effect of temperature on femur length, tibia length, wing length, and wing breadth of *Drosophila*, as well as on longevity, was analyzed. It was shown that flies developing at 18° are larger than those developing at 28° in respect of all four measurements. Alpatov (1932) showed that both the length and breadth measurements of the wings of wild-type *Drosophila* were smaller if the larvae were underfed or reared at high temperature. Harnly (1930) reported somewhat different results for vestigial *Drosophila* males. Hammond (1939, p. 47) summarizes these data as follows: "... in vestigial males a rise in temperature from 18.3°C. to 29.0°C. produced a very slight *lengthening* of the wings; between 29°C. and 30°C. the wings increase 25 per cent in length, and from 30° to 31°C. they increase 70 per cent in length."

Before concluding this discussion of action a word of caution is necessary. The reader should not get the impression that temperature and relative humidity are the only habitat factors known for experimental populations, or for that matter and quite obviously, for natural populations. We have stressed these two cases for illustrative purposes. They provide good examples of the actions they

depict and are probably as direct and uncomplicated as any that could be found. We shall not forget the important rôle of habitat action in passing on to consider other factors; rather, it will be our hope to continually relate it to the general ecological system of Clements and Shelford. We shall particularly stress action as a corollary of reaction in the next section.

### *Reaction*

Reaction has been defined and discussed as the effect of the community on the habitat. It has been shown that actions and reactions go on continuously within any biological grouping and that they constitute the primary cycle of cause and effect. At this place we wish to illustrate reaction as it exists in laboratory populations. This means that cases must be found where it can be demonstrated that the population impinges an effect or reaction upon the habitat or physical-chemical environment.

*Tribolium.* For *Tribolium* there are a number of reactions that are immediately obvious. For, example, the beetles tunnel through the medium thus altering its topography and comminute the particles of flour and meal by the grinding action of their mouthparts. However, these are somewhat in the category of less important effects. We wish to examine here a more complex reaction system that can be shown of significance in controlling the integration and growth of the entire population. I have been interested for some time in analyzing a *Tribolium* population problem that I have called the "conditioned flour problem." A series of papers on this subject have appeared (see Park, 1934, 1935, 1936, 1936a, 1937, 1938, 1938a, 1939; Park and Woollcott, 1937; Park, Miller and Lutherman, 1939; Stanley, 1934; Ford, 1937). The present report is not concerned with reviewing in any detail these studies but, rather, will attempt to show that this problem in its broader aspects has application to the ecological system under analysis. This application must be made in several places in the paper; it cannot be disposed of under the heading of reaction alone. However, there are enough phases of reaction inherent in the conditioning work to warrant its introduction here.

A brief background is in order. Conditioning illustrates a population effect operating primarily through alteration of the habitat. If *Tribolium* populations are allowed to age without experimental disturbance of the flour in which they live they gradually become extinct and the flour noticeably changes in chemical and physical composition. This change in the medium is spoken of as biological conditioning. "Conditioned flour" thus is a substance which is produced by the beetles in their normal course of living. It is an inevitable product of *population activity* owing its existence entirely to the cumulative effects of the breeding and general behavior of the beetles themselves. More specifically, conditioned flour differs from fresh or unconditioned flour in that the beetles inhabiting it have reduced its nutritive value through constant feeding and have added certain by-products such as excretory wastes and frass not present in the original medium.

Several points are immediately apparent. First, the processes just described as occurring during conditioning are obviously not all reactions. Second, conditioning is of no real significance unless it affects in turn the development of the population. These points merit examination. It has been shown that a *Tribolium* population alters through its own activity the habitat by reducing the nutritive level and adding certain by-products to the

medium. What ecological processes are concerned with this conditioning? I think it can be safely said that action, reaction, and certain coactions are all functional. A question immediately arises: shall the alteration of the flour (habitat) caused by conditioning be called reaction or disoperation? It is reaction in the sense that the population has modified the habitat; disoperation in the sense that through coactions an effect is produced on the habitat that is deleterious in terms of the total population. There are also a series of definite actions since conditioned flour, whether produced by reaction or disoperation or both, affects markedly the development and reproduction of the beetles. There is risk here in getting bogged down in the terminology without accomplishing anything constructive. This is done too frequently in ecological writing and certainly should be avoided in this paper. For purposes of expediency, let us assume temporarily that conditioning illustrates reaction and proceed from that point.

In terms of the population it is meaningful to examine conditioning as an environmental factor that initiates action. The position is this: we know that conditioned flour is a population product; we know something, though far from all, of its nature; how does this biotically altered medium affect the physiology of *Tribolium* and thereby the development of the population? This seems a logical approach since it facilitates the analysis of the primary cycle of cause and effect, action-reaction, under one treatment.

Following are some of the actions of conditioned flour on the physiology of *Tribolium* (Park and Woollcott, 1937):

(1) It reduces their cannibalism (i.e. the rate at which imaginal beetles eat their own eggs) to about half that of control beetles living in fresh flour. This is an example of an action (conditioning acting on the beetles) followed by a reduction in competition for eggs (i.e. lowering of the rate of egg consumption).

(2) It reduces their fecundity drastically —lowering it three or more times below a control level by reintroduction of the beetles into fresh or unconditioned flour. It also reduces the fecundity of virgin (i.e. non - fecundated) female beetles. These are probably cases where conditioning acts directly on the beetles with no important secondary coactions.

(3) There is some evidence that conditioning affects fecundity through the males as well as through the females since in one group of experiments the data showed that females reared in fresh flour when mated with males reared in conditioned flour had a lower rate of reproduction that did control (fresh) males mated to control females. In this case the action appears to be first on the male reducing in some way his sexual efficiency. The male's effect on the female represents some form of coaction.

(4) Conditioning increases the relative variability of *Tribolium* fecundity. This is probably another case of uncomplicated habitat action working directly on the physiology of the ovipositing female.

(5) Conditioning apparently does not alter in any consistent pattern the fertility of the eggs. In other words, once produced, eggs from conditioned-flour beetles have about as good a chance of hatching as do eggs from fresh-flour beetles. This is another way of saying that, while the conditioned flour markedly lowers egg fecundity, it has no action on egg hatchability. Thus, reproductive effects in the population caused by conditioning are fecundity rather than fertility effects.

(6) It increases the duration, variability, and mortality of larval metamor-

phosis. There is evidence that the major factor in this case is the direct action of conditioned flour on the larvae. Competitive coactions, other than those involved in actually conditioning the flour, appear unimportant. It has been shown (Park, 1938; Park, Miller and Lutherman, 1939) that if the larvae are cultured in dense populations with the flour experimentally kept from getting conditioned no lengthening of the larval period or increase in larval mortality is observable. In this case there would be many coactions in the crowded cultures but they would be essentially unimportant in causing the type of metamorphosis effects observed for conditioned populations.

A final question is this: what is the summed effect of these actions on the development of the total population? The answer is clear for two reasons: first, all described conditioning effects are either indifferent (fertility) or deleterious (fecundity reduction, lowered rate of metamorphosis, increased larval mortality), and second, the medium is conditioned in direct proportion to the age of the culture. This means that populations of *Tribolium* will gradually decline and eventually become extinct due to the accumulation of conditioned flour and the action of this flour on the beetles' physiology.

In summary, it can be repeated that (1) conditoned flour is a habitat modified by the reaction and disoperative effects of the total *Tribolium* population; (2) this habitat has certain known actions on the population and its constituents that lower the beetles' productivity and developmental efficiency; and (3) conditioning, working through these physiological processes, brings about the decline and eventual extinction of the population. We shall return to selected aspects of the conditioned flour problem later. It seems unnecessary to labor the point that this analysis based on laboratory research has direct application to natural communities when interpreted in the light of the Clements-Shelford concepts. Though simplified, laboratory populations are total communities.

*Drosophila.* *Drosophila* population studies have concerned themselves largely with coactions. This will be discussed later. There are no analyses to my knowledge that can be used as illustrations of reaction. A few possible reactions can be imagined but their significance, if any, has not been tested experimentally. An obvious case is the burrowing of the maggots in their substratum. This is probably a reaction of some importance since *Drosophila* larvae must develop in a moist habitat such as that provided by tunnels in the agar. It is also possible that the fly population reacts on its environment in some way analogous to conditioning in *Tribolium*. This is a fertile field still open for attack and its importance is suggested by a statement of Bodenheimer (1938). This author is concerned with the growth of a total population of a Palestine strain of *Drosophila*. He divides this growth into three periods: Period of Initial Growth (0–9 days); Period of Rapid Growth (10–14 days); Period of Oscillations (15–22 days); and Period of Contraction (23–35 days). In discussing the last phase Bodenheimer says,

> "The final contraction [of the population] is therefore not due to the intra-specific struggle for existence [coaction], but some intoxication, especially effective in the adult stage. The enormous mortality following hatching of new flies during the latter part of this period before the end of their first day of adult life points to this direction. Population pressure is certainly not involved in this adult mortality, or only to an inconsiderable extent. More detailed studies are needed before any explanation may be given. The form of decrease agrees with that of a moderate intoxication curve" (p. 76).

It is probable that this "intoxication" effect will prove to be a potent action-reaction or disoperative system when finally analyzed. It is hoped that this analysis will be forthcoming soon.

*Tenebrio.* Michal (1931) reported that a population of meal-worms (*Tenebrio* larvae) raise the temperature and humidity of their medium. This is a diagrammatic illustration of reaction—the population modifies the physical-chemical habitat to a noticeable degree.

One reason for working with experimental populations lies in the fact that frequently they permit refinements to be made in the analysis of environmental relations that can only be approximated in the field. Typically, in dealing with natural populations one can merely name a process, say, as an action or reaction without understanding its various degrees of complexity. This complexity may build up with time as both the habitat and the population change. The older population still has internal phenomena that properly are actions and reactions but they are different and usually more intricate. These "higher order" factors can be studied and experimentally dissected. In this point lies one of the merits of the laboratory population as an ecological tool. An example will make the point. We conclude that conditioned flour is a product of reaction and disoperation and that, through these mechanisms, a modified habitat results. This habitat acts back on the population with definite end-results. The cycle is not completed here, however, for as the culture matures, coactions as well as reactions increase in intensity and in type and the habitat suffers further modification. And so the story goes. In many cases this chain of events can be analyzed in the laboratory better than it can in the field.

*(To be concluded)*

# COMPARATIVE ANATOMY AND PHYSIOLOGY OF THE ANTERIOR PITUITARY

By AUBREY GORBMAN
*University of California*

## INTRODUCTION

TOPOGRAPHICALLY, the pituitary gland occupies one of the most protected positions in the vertebrate organism. In the evolution of species, however, it would seem that a structure concerned with so many vitally important physiological processes must be subject to severe phylogenetic "stresses." In some instances new "target organs" have been brought under the sphere of influence of the pituitary (e.g. the mammary glands) or old ones have virtually disappeared (e.g. melanophores in adult birds and mammals). Furthermore, in some instances evolution has wrought an extreme anatomical or functional change in one of the pituitary "target organs." This is the case with the pliable vertebrate genital system. The appearance of corpora lutea in reptiles and mammals, the suppression of yolk deposition in the maturing egg, the progression from oviparity to ovoviviparity and viviparity, and the differentiation of types of protein metabolism according to the kind of egg laid (cleidoic or non-cleidoic)—all of these may be reflections of qualitative or quantitative changes in hypophyseal secretions. Frequently, even within relatively small animal groups, the target organ has been shown to vary between species in the temporal spacing of its periods of functional activity and rest. Have there been corresponding changes in the pituitary? To the comparative physiologist the changes in the relationship between the pituitary and the structures influenced by its secretions present an absorbing, and as yet an incompletely understood problem.

Morphological studies of the pituitaries of many vertebrates have been in progress for some time, and some especially thorough work has been done in the mammals and birds. Unfortunately, most of this work has been primarily exploratory, and the summarized data allow generalizations only in regard to the more gross features of hypophyseal anatomy. Work with fish, amphibia, and reptiles does not yet provide an adequate basis for a functional interpretation of observed morphological features. There is even less justification at the present time for declaring the functional equivalence of certain parts of the pituitary in different lower vertebrates.

In all vertebrates the pituitary is formed by the union of a lobe of the floor of the brain with a lobe or vesicle of somatic ectoderm, which migrates inward from the oral epithelium or (in cyclostomes) from the ectoderm of the upper lip. The lobe of somatic ectoderm then becomes further differentiated into an intermediate, or juxta-neural region (secondarily lacking in birds), and an "anterior" or distal

part. In many animals there is also differentiated a pars tuberalis, which is situated dorso-laterally in respect to the rest of the gland and is most often applied to the infundibular stalk. In teleosts and cyclostomes Stendell (1913) named a region between the pars intermedia and pars distalis, the *Übergangsteil*. The problem of the functional and anatomical status of the *Übergangsteil* has provoked considerable discussion, but its solution awaits physiological experimentation. In elasmobranchs, pituitary structure reaches its greatest apparent complexity with the addition of a "ventral lobe" extending ventrad from the base of the pars distalis. The nature of this lobe as is the case with some other parts of the elasmobranch pituitary, is not clear.

*Pituitary homologues in the invertebrates*

In the most primitive of living vertebrates, the cyclostomes, there is, according to Tilney (1937), already a well-developed pituitary consisting of pars nervosa, pars intermedia, pars tuberalis, *Übergangsteil*, and pars distalis. It is difficult to conceive how this organ, having such diverse anatomical and physiological properties, can have had its sudden inception in the vertebrates. It seems probable that the pituitary gland as we know it is the product of a considerable, and still wholly unknown, evolutionary history. Many have attempted to find structures comparable to the pituitary in the lower chordates, in the arthropods, and in the echinoderms, each of which is believed by some zoologists to bear an evolutionary relation to the vertebrates.

Perhaps the most reasonable suggested invertebrate homologue is the subneural gland of urochordates, which has been described by early workers as an excretory organ. This homology has had such distinguished promulgators as Éd. van Beneden (1884) and W. Bateson (1886). In these animals the gland, which is usually median, but may be bilateral, is most often located ventral to the ganglionic "brain" and communicates through a ciliated duct with the posterior part of the mouth (Delage and Hérouard, 1898). The urochordates are so degenerate, and have so unusual a developmental history, that it is difficult to evaluate this suggestion on the basis of the few anatomical similarities seen between the subneural gland and the vertebrate pituitary. However, the discovery that extracts of subneural glands have pressor and oxytocic activity, and melanophore-dilating action in frogs seems highly significant (Bacq and Florkin, 1935). Hogg (1937) declares that he has produced mild ovarian stimulation in mice with extracts of ascidian (*Polycarpa tecta*) subneural gland. Benazzi (1939) could not confirm this finding in tests in which he administered as many as 200 *Ciona intestinalis* subneural glands to young rats, or 450 glands to an adult female salamander, *Triton cristatus*. On considerably less evidence various structures in other protochordates have been suggested as homologues of the vertebrate pituitary. In the Hemichordata three different organs have been indicated, on morphological grounds, as related to the pituitary: (1) the proboscis pore, a dorsal opening of the coelomic cavity within the proboscis (Bateson, 1886; Willey, 1899), (2) the notochord, an anterior evagination from the mouth into the proboscis (Harmer, 1897; Masterman, 1899), and (3) the preoral ciliary organ, a crescentic band of ciliated cells on the posterior surface of the proboscis (Brambell and Cole, 1939). In these animals the homology is therefore far from clear. On similar grounds the preoral pit (Bateson, 1886) or the preoral pit plus the olfactory pit (Willey, 1899) represent the

hypophyseal homologues in Cephalochordata (*Amphioxus*). Even the anterior nephridial tubes (Legros, 1909) and the taste buds (Tretjakoff, 1929) of *Amphioxus* have been involved in this fertile speculative field. The eye-stalk of the crustacea, from which may be extracted a melanophore-dilating hormone (Abramowitz, 1937) and a hormone causing accumulation of water in frogs (Gray and Ford, 1940), and the corpora allata of insects which seem to have a gonadotropic effect in insects (Pfeiffer, 1939) have been shown to have pituitary-like functions, but their homology is extremely questionable. At any rate it remains to further work to determine whether the occurrence of chromatophorotropic substances in eye-stalk and subneural gland extracts, is of any greater significance from the point of view of homology than the finding of sex hormones in non-homologous organs in invertebrates, or in plants.

*Comparative gross morphology of the pituitary*

The recent careful work of Tilney (1937) on the pituitary of *Petromyzon* has definitely established its complex nature in the lampreys. The large "hypophyseal canal" which is still described in recent textbooks (1939) has been declared by Tilney to be an artefact, and not the primitive "anterior lobe." No suitable study making use of improved modern techniques has ever been made of the hypophysis of the hagfish, the only other type of living cyclostome. Both Stendell (1913) and De Beer (1926) have made the interesting claim that the pituitary in hagfishes consists of no more than a number of patches of undifferentiated cells beneath the infundibulum. It is surprising that this claim, which would establish the hagfish pituitary as different from that in the entire class Vertebrata, has not stimulated further investigation. In some recent preliminary work with the Pacific coastal hagfish, *Polistotrema* (*Bdellostoma*) *stouti* the writer has been able to confirm, in general, the statements of Stendell and De Beer. Study of the skeleton of the extinct primitive cyclostomes, the cephalaspid ostracoderms, has revealed a median pore on the dorsal side of the head, which Patten (1912), Stensiö (1927), and others call the "hypophyseal pit." If this identification is correct, then the extrabuccal derivation of the epithelial hypophyseal lobe in cyclostomes may be assumed to have had an early origin, and might be the primitive mode of origin for all vertebrates. Embryological studies in amphibia in which the hypophyseal anlage may be traced from an originally dorsal to a finally ventral position make such a mode of origin easily explicable.

It may be concluded from Tilney's studies that the common Ordovician ancestor of the Cyclostomata and the higher fishes must have had an organized pituitary. In the light of existing information it seems highly improbable that a satisfactorily complete history of the organization of the anatomical and physiological pituitary complexes will ever become available.

The changes of the pituitary within the class Pisces have been even more diverse than those within the entire group of higher vertebrates. The pituitary of of elasmobranchs is entirely unlike that of other fish. In fact it resembles the gland of higher vertebrates even less than does the pituitary of *Petromyzon*. However, within the elasmobranch group the hypophysis is quite uniform and Norris (1936) who made a study of 72 species, found that certain minor differences were correlated with taxonomic groupings. Two main types of elasmobranch pituitary could be distinguished, a selachoid (shark) and

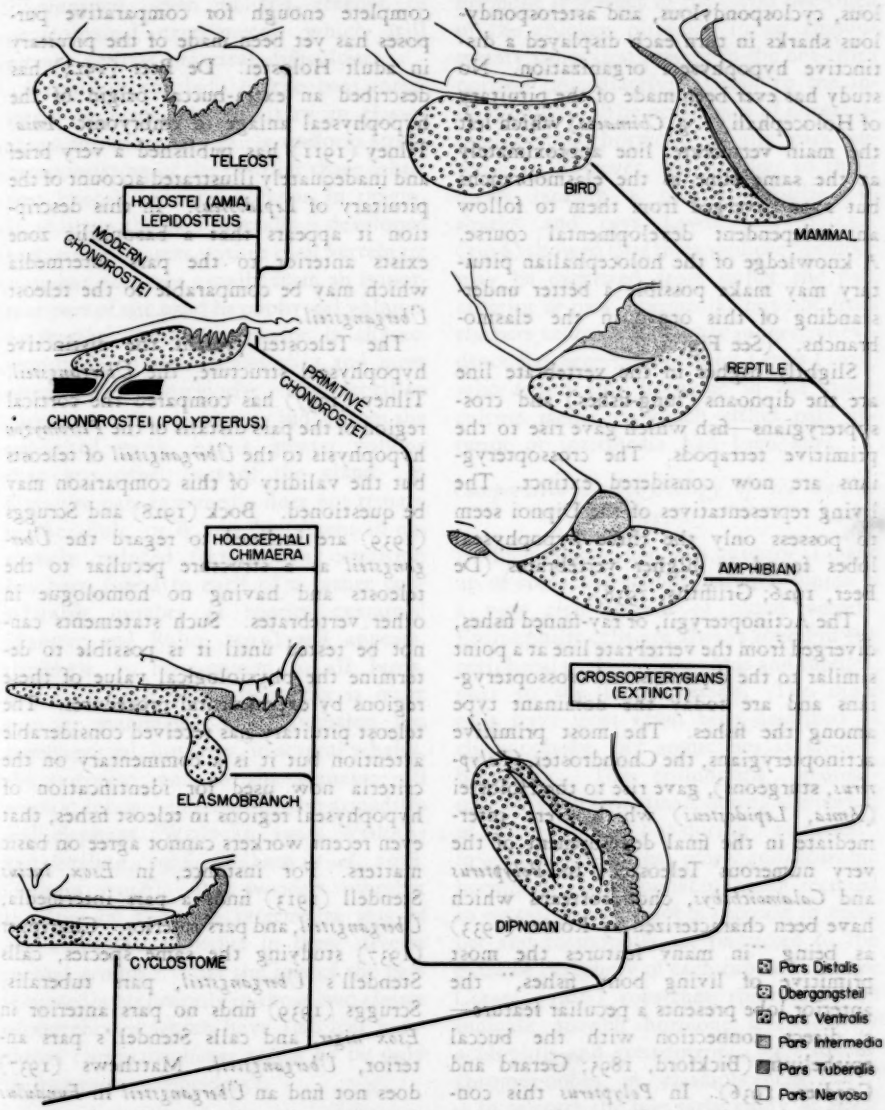



FIG. 1. PHYLOGENESIS OF THE VERTEBRATE PITUITARY

All drawings are schematic diagrams, not intended to accurately represent any single species. Drawing of dipnoan based on Griffiths (1938). Drawing of cyclostome based on Tilney (1937).

a batoid (ray) type. The diplospondylous, cyclospondylous, and asterospondylous sharks in turn each displayed a distinctive hypophyseal organization. No study has ever been made of the pituitary of Holocephali (e. g. *Chimaera*) which left the main vertebrate line approximately at the same time as the elasmobranchs but soon diverged from them to follow an independent developmental course. A knowledge of the holocephalian pituitary may make possible a better understanding of this organ in the elasmobranchs. (See Fig. 1.)

Slightly higher in the vertebrate line are the dipnoans (lung-fishes) and crossopterygians—fish which gave rise to the primitive tetrapods. The crossopterygians are now considered extinct. The living representatives of the Dipnoi seem to possess only the three hypophyseal lobes found in higher vertebrates (De Beer, 1926; Griffiths, 1938).

The Actinopterygii, or ray-finned fishes, diverged from the vertebrate line at a point similar to the dipnoans and crossopterygians and are today the dominant type among the fishes. The most primitive actinopterygians, the Chondrostei, (*Polypterus*, sturgeons), gave rise to the Holostei (*Amia*, *Lepidosteus*) which were intermediate in the final development of the very numerous Teleostei. In *Polypterus* and *Calamoichthys*, chondrosteans which have been characterized by Romer (1933) as being "in many features the most primitive of living bony fishes," the anterior lobe presents a peculiar feature—a direct connection with the buccal epithelium (Bickford, 1895; Gerard and Cordier, 1936). In *Polypterus* this connection is a short hollow stalk opening directly into the mouth cavity and displaying at its upper end a transitional zone of cells from the epithelial to the hypophyseal type. The position of this stalk suggests a comparison with the ventral lobe of elasmobranchs. No study complete enough for comparative purposes has yet been made of the pituitary in adult Holostei. De Beer (1923) has described an extra-buccal origin of the hypophyseal anlage in embryonic *Amia*. Tilney (1911) has published a very brief and inadequately illustrated account of the pituitary of *Lepidosteus*. In this description it appears that a basophilic zone exists anterior to the pars intermedia which may be comparable to the teleost *Übergangsteil*.

The Teleostei present the distinctive hypophyseal structure, the *Übergangsteil*. Tilney (1937) has compared the cortical region of the pars distalis of the *Petromyzon* hypophysis to the *Übergangsteil* of teleosts but the validity of this comparison may be questioned. Bock (1928) and Scruggs (1939) are inclined to regard the *Übergangsteil* as a structure peculiar to the teleosts and having no homologue in other vertebrates. Such statements cannot be tested until it is possible to determine the physiological value of these regions by experimental procedures. The teleost pituitary has received considerable attention but it is a commentary on the criteria now used for identification of hypophyseal regions in teleost fishes, that even recent workers cannot agree on basic matters. For instance, in *Esox lucius* Stendell (1913) finds a pars intermedia, *Übergangsteil*, and pars anterior. Charipper (1937) studying the same species, calls Stendell's *Übergangsteil*, pars tuberalis. Scruggs (1939) finds no pars anterior in *Esox niger*, and calls Stendell's pars anterior, *Übergangsteil*. Matthews (1937) does not find an *Übergangsteil* in *Fundulus heteroclitus*, but Scruggs (1939) characterizes this structure as well developed in the same species. The apparently sudden appearance of the *Übergangsteil* in teleosts indicates the need of study of the holostean pituitary. Such study may prove of in-

terest in determining the status of the *Übergangsteil*, even in the absence of physiological experiments, which still present serious practical difficulties.

Excepting the lack of the pars intermedia in birds, the pituitary in classes above the fishes is a fairly uniform structure consisting of the familiar three lobes, two buccal and one nervous in origin. In addition the pars tuberalis is developed to variable degrees within each vertebrate class but does not usually form an important part of the total hypophyseal volume. In reptiles the pars anterior is characteristically elongated and thin and most often curves anteriorly. The reptilian pars intermedia, if we may judge from the published work, has a greater volume than any other part of the gland. In birds the pars intermedia does not remain in the adult, or it may be present in extremely reduced form. This condition has been found in each of a rather considerable number of species examined (Painter and Rahn, 1939) and appears, therefore, to be common to all birds. The lack of a pars intermedia is quite rare in mammals. This condition has been reported, however, in several whales, the porpoise, and in the manatee—all aquatic forms—and also in the armadillo and elephant (Wislocki, 1929; Wislocki and Geiling, 1936; Oldham *et al*, 1938; Oldham, 1938). One wonders whether the loss of the pars intermedia was of any evolutionary value in these diverse animal groups. That the loss of the pars intermedia occurs only in those two classes of vertebrates which have also lost functional chromatophores seems to be only an interesting coincidence.

### *The site of production of melanophore hormone*

It is a fact that in those animals which have no pars intermedia the melanophore hormone is found in the pars anterior. Even more surprising is the finding of Kleinholz and Rahn (1939) that this hormone is present in the distal one-third of the chicken pituitary in an amount twenty times that present in the one-third portion immediately adjacent to the infundibulum. The occurrence of chromatophorotropic hormone in the pars anterior is, however, not peculiar to those forms lacking a pars intermedia. In sharks and rays Lewis and Butcher (1936) showed that melanophore hormone may be extracted from either the pars anterior or pars intermedia, but not from the pars ventralis. Highly suggestive evidence has been presented by Lewis (1936) who found this hormone in the tissue culture media in which either pars anterior or intermedia had been kept.

### *Comparative histophysiology of the anterior pituitary*

The elasmobranch pars anterior is made up of cords and tubules between which is a very rich system of blood vessels. Eosinophilic cells are always found in the peripheral parts of these cords and tubules, next to the blood vessels. The inner cells have most often been described as chromophobe, but sometimes as weakly basophilic. The eosinophils predominate in younger animals during the period of active growth, but during "gestation" in viviparous sharks, when gonadotropic hormones are presumably being secreted in excess, chromophobes increase in number and eosinophils are restricted to the extreme periphery of each tubule. Carere Comes (1936) construes these data to indicate growth hormone secretion by acidophils and gonadotropic secretion by chromophobes in elasmobranchs.

In teleosts the fine early study of Bock (1928) of the pituitary of the Stickleback represents the only histophysiological work in bony fishes. Bock found no typical basophils in the pars anterior—only acidophils and chromophobes. The

same was true of the *Übergangsteil*. Using degranulation as an index of secretory activity, the pars anterior was found to exhibit no cyclic change throughout the year. The *Übergangsteil*, however, was rapidly degranulated in June and July. Acidophil granules were then slowly restored and reached a maximum level again in November and December. Unfortunately, no significant conclusions can be drawn from these facts until they can be correlated with more definite physiological activities.

In Amphibia Zahl (1935) has made similar cytological observations of the frog pituitary during the seasonal sex cycle. In frogs there is a gradual increase in acidophilic granules during the winter months. In the spring a sudden degranulation of acidophils occurs, during the period of sexual activity. Gonadotropic activity of the glands, when tested by the implant method by Zahl, appears to be correlated with a greater degree of granulation of acidophils. This work, if it can be said to locate gonadotropic hormone (reference is made to the primary or follicular stimulating component of the gonadotropic complex), production in the acidophils, is in apparent disagreement with the more firmly established data in birds and mammals. Thyroidectomy in the salamander *Triturus* produces a more orthodox result, namely vacuolization of basophils (Grobstein, 1938).

The anterior lobe of reptiles, like that of amphibia contains acidophils, basophils, and chromophobes. According to Altland (1939), basophilic cells increase in number during the breeding period of the lizard and may therefore be involved in gonadotropic secretion. During the remainder of the season the anterior lobe is predominantly acidophilic. Thyroidectomy in the snake (Siler, 1936) leads to enlargement and vacuolization of basophils. In time these enlarged basophils become chromophobic and finally pycnotic.

Schildmacher (1937) has made a study of seasonal cytological changes in the anterior lobe of the robin *Turdus merula*. Basophils and chromophobes appear to remain uniform throughout the year, but eosinophils are found in significant numbers only during the spring breeding period. Schooley and Riddle (1938) have reported a rather complete histophysiological study of the pigeon pituitary. By correlating cytological structure with periods of growth, gonadal activity, brooding, and bioassays of hormone activity during these periods, they concluded that the acidophils are responsible for this "growth" effect and for crop-sac stimulation. Basophils can be correlated with gonadotropic and thyrotropic activity.

In summarizing the data purporting to reveal the physiological rôles of the different tinctorial cell types of anterior lobes of the lower vertebrates, it must be admitted that nothing but suggestive information now exists, excepting the somewhat better work in birds. The unsettled nature of these questions should invite further study, since existing data seem to indicate that in different species, even within a single class, different tinctorial cell types may be responsible for the formation of the same hormone.

### *Known occurrence of pituitary hormones*

Many hypophysectomies have now been made in the lower vertebrates, and still more pituitary-injection experiments have been conducted in exploration of the extent of hypophyseal action in the various animal groups. This information has been summarized in Table I. However, certain unusual results obtained in

TABLE I

*The known occurrence of pituitary hormones*

| | CHROMATOPHOROTROPIN | GONADOTROPIN | THYROTROPIN | ADRENOTROPIN | GROWTH | PROLACTIN | DIABETOGENIC |
|---|---|---|---|---|---|---|---|
| Crustacean eye-stalk | + (2) | : | : | : | : | : | : |
| Insect corpus allatum | : | + (92) (73) | : | : | : | : | : |
| Ascidian subneural gland | : | + (44) − (13) | : | : | : | : | : |
| Cyclostome | + (99) | : | : | : | : | : | : |
| Elasmobranch | + (58) (2) | : | : | : | : | : | : |
| Teleost | + (1) | + (46) (21) (49) (9) LH (97) | + (37) | : | : | +? (32) | : |
| Amphibian | + (Many reports) (1) | + (Many reports) (48) (98) (27) | + (85) (5) (4) | + (20) (74) | +? (34) | +? (32) (35) | + (47) (84) |
| Reptile | + (30) (1) | + (46) (78) | + (78) (43) | : | : | +? (32) | : |
| Bird | + (32) (51) | + (Many reports) FSH (54) (65) LH (96) (54) | + (96) (86) (37) | + (65) | + (Many reports) | + (32) (80) − (65) | : |
| Mammal | + (Many reports) | + (Many reports) FSH (Many reports) LH (Many reports) | + (Many reports) | + (Many reports) | + (Many reports) | + (Many reports) | + (Many reports) |

lower vertebrates deserve more than passing mention.

*Comparative physiology of gonadotropic hormones*

Since the establishment in mammals of separate luteinizing, follicle-stimulating, and other gonadotropic hormones, it has become of interest to determine the action of such fractions in gonads differing greatly from mammals in structure, and gonads lacking typically mammalian parts, like the corpus luteum. Conversely, the comparative physiologist wishes to learn whether the pituitary of lower vertebrates is capable of acting on structures which were evolved at a later time, in response to reproductive needs of a different sort. In *Triturus*, a salamander, FSH is considerably more effective in stimulating growth of ovaries in hypophysectomized animals than is LH; LH, on the other hand, is a considerably more effective reagent in inducing ovulation (Mayo, 1937). Amphibian pituitaries in mammals have never been given in high enough dosage to produce results of any note. Doses of 211 frog pituitaries (233 mg) produced only slight gonadal and uterine stimulation (in weight) in the mouse (Adams and Granger, 1938). Doses of 8 to 20 mg of African clawed-toad pituitary produced slightly more pronounced effects in immature mice (Zwarenstein, 1939). Such treatment gave *blutpunkte* and slight ovarian weight stimulation, opening of the vagina, and a two- to four-fold increase in weight of the uterus. The meager information provided by these experiments seems to indicate that amphibian pituitary contains a gonadotropic substance capable of acting in mammals, but its more exact nature cannot be determined without larger dosages of amphibian pituitary. It would seem from Mayo's work that the amphibian ovary, aside from the fact that it lacks a corpus luteum, responds quite similarly to the mammalian gonad to FSH and LH. However, the action of FSH in amphibia, although involved in the same *phase* of ovarian function, is actually producing a different end result. FSH in mammals stimulates follicular growth. FSH in amphibia, according to Mayo's work, stimulates *growth and maturation of the ovum*, which in mammals is a process which apparently proceeds independently of pituitary action. The work of Mayo on this important question deserves careful and extensive checking with more studies on hypophysectomized amphibia. In view of the finding that mammalian ovulation occurs after LH administration to females with ripe follicles the data of Mayo are quite regular. However, when one considers that ovulation is the only response of which a mature amphibian gonad is capable, and that human pregnancy and menopause urine, pregnant mare's serum, and pituitary preparations from many mammals have been successfully used to elicit this response, it seems that ovulation may not be so specific a reaction in amphibia after all. Even more surprising in this regard have been the recent publications of Shapiro (1939) and Zwarenstein (1937), who showed that ovulation in hypophysectomized *Xenopus*, the clawed-toad, can be induced by progesterone and a number of natural and synthetic androgens, but not by estrogens. They could even produce release of ova by adding these hormones to *in vitro* preparations of excised *Xenopus* ovary.

Mammalian pituitary FSH, LH, and gonadotropic antagonist preparations, and pregnant mare serum extract increase ovarian vascularity and increase ovarian weight by yolk deposition in the Horned toad (Mellish and Meyer, 1937). Rep-

tilian pituitary, on the other hand, has never been tried in the mammal. The ability of the various different mammalian gonadotropic fractions to stimulate growth of the ova would seem to indicate that this response may be as non-specific as ovulation appears to be in *Xenopus*. However, this possibility must be tested in hypophysectomized animals. L. T. Evans (1935) has found that urinary prolan and sheep pituitary extract also stimulate ovarian growth in *Anolis*, but only the hypophyseal preparation will induce ovulation. Rahn (1939) has recently published good descriptions of the corpora lutea of various reptiles. It is unfortunately true that none of the recent workers using relatively purified gonadotropic fractions in reptiles has made observations on the physiology of the reptilian corpus. Cunningham and Smart (1934), using rather impure preparations of beef pituitary, stimulated ovulation in two viviparous lizards (*Anguis*, and *Zootoca*) and in one oviparous lizard, *Lacerta*. Corpora lutea were then found to develop in the two viviparous species. This work makes it especially desirable that the gonadotropic properties of reptile pituitaries be thoroughly investigated, since such work may shed some light on the problem of evolution of separate gonadotropic fractions. Several authors (Table I) have recently succeeded in finding LH in bird pituitaries, and since, according to some of these workers, the bird has no corpora lutea, LH appears phylogenetically before the corpus luteum itself. This statement may be questioned from two standpoints; (1) Mingazzini (1893), Cunningham and Smart (1934) and others have demonstrated the existence of a corpus in an ancestral group—the reptiles; (2) the birds themselves are at the end of an evolutionary line, so that the appearance of LH in this group does not anticipate any events in any other group of vertebrates. Since the reptiles were also the ancestral group for the Mammalia, corpora lutea in these two classes are probably homologous, and to find the origin of hypophyseal control over these new structures it seems now that we must investigate not only the reptilian pituitary but also that of more primitive forms. Recently Witschi (1939), has reported, in abstract, the occurrence of LH in the pituitary of the salmon, using a test based on a reaction of the regenerating feather of the Weaver-finch. If the validity of this finding can be confirmed by stimulation of luteinization in the usual assay procedures it would indeed be established that LH has arisen long before the organized corpus luteum. The possible function of a luteinizing hormone in the lower vertebrates presents many interesting possibilities. The apparent diversity of the action of LH on the amphibian ovary (Mayo, 1937) and on the feather of the Weaver-finch indicates that this problem probably has no simple solution.

FSH and LH in birds produce, respectively, germinal and interstitial cell stimulation, as they do in mammals. The very adequate researches of Witschi *et al.* (1937) and Meyer, Mellish, and Kupperman (1939) have demonstrated that turkey and chicken pituitaries both contain FSH and LH. It is more or less surprising to find that the bird gonad is especially non-responsive to prolan, when the gonads of certain fish, amphibia, and reptiles can be stimulated by this substance.

### *Thyrotropic, adrenotropic and lactogenic hormones*

As far as they have been studied, the thyrotropic and adrenotropic hormones, as well as their target organs themselves, have been quite uniform throughout the vertebrates and do not seem to offer any

important problem to the comparative physiologist. However, it might be of interest to investigate the action of thyrotropin and adrenotropin in the ammocoetes of lampreys, since the target organs in these animals present certain peculiarities.

Prolactin occupies a peculiar place in comparative endocrinology at the present time since Leblond and Noble (1937) have reported it in the pituitaries of every vertebrate class from the fishes on, and its target organ, the mammary gland, is not evolved until the mammals. Leblond and Noble, using Lyons' method of assay, obtained some results with fish, amphibian, and reptilian pituitaries which they themselves characterized as "prolactin-like" because they were not entirely typical. As many as fifty to one hundred fish pituitaries (*Ameiurus*) implanted subcutaneously at one site were required to give a "positive" test. Chicken pituitaries in their hands gave a rather strong prolactin reaction to a considerably smaller amount of pituitary tissue, but Meyer, Mellish, and Kupperman (1939) using the same test and the same pituitary source obtained negative results. Nevertheless, the action of this hormone in lower vertebrates should be examined very carefully, especially now that it is available in comparatively purified form. Noble, Kumpf, and Billings, (1938) found that prolactin induced brooding behavior in the Jewel-fish (*Hemichromis bimaculatus*), although progesterone was even more effective in this respect. These investigators did not look for any other effect of prolactin in the fish. Chadwick (1940) has recently identified prolactin as the hormonal stimulant for "water-drive" in the land stage *Triturus viridescens*. Any explanation of the presence of prolactin in the pituitaries of the lowest vertebrates is no more than a guess, but it might be profitable in this case to venture a reasonable guess to indicate the manner in which this problem might be attacked. It could be that prolactin has a still unrecognized function, perhaps serving as (1) a parental or "care of the young" hormone, in lower vertebrates, or (2) since it is of such general occurrence, and since Riddle seems to have shown its close relation to the growth effect, it might serve as a special growth hormone affecting definite organs, like abdominal viscera. The recent chemical data of Evans (1939) and his co-workers appear to rule out any possibility of identity of prolactin with the classical growth hormone.

### *Instances of unusual actions of pituitary hormone*

We are accustomed to regard the secondary and accessory sex characters of vertebrates as being subject to the control of the gonadal hormones. Yet there are at least three instances in lower vertebrates in which such characters have been claimed under the direct influence of hypophyseal hormones. Guyenot, Moskowska, and Ponse (1932) found that the nuptial thumb pads of male toads, *Bombinator pachypus*, could be stimulated in castrate animals by pituitary implants. It is known that in other amphibia this structure can be stimulated by the pituitary only in the presence of an intact testis. De Allende (1938) using another toad, *Bufo arenarum*, has published the surprising statement that pituitary implants will stimulate secretory activity in the oviduct of castrates, but *large doses of estrone will not!* Finally, Witschi (1937) has demonstrated that pituitary preparations can induce cock-feathering in castrate African finches (*Pyromelana*, *Steganura*, or *Quelea*). His data seem to indicate that LH is directly responsible for this effect, and in fact he suggests the use of such birds for the bioassay of LH.

*Environmental influences on the pituitary*

We have been considering at some length the control by the pituitary over certain secondary organs and processes in the vertebrates. We must now consider the factors which have been found to stimulate activity of the pituitary. This problem is especially important in the understanding of those conditions in which cyclic changes in pituitary activity have been found to occur. In most vertebrates this cycle is annual. In mammals shorter oestrous cycles may be superimposed on the annual cycle. In some cases, as in the rat and in man, the annual cycle may be lost. At least a part of the factors involved in these regular fluctuations of endocrinal activity are now understood—primarily from work with birds by Marshall (1936), Bissonette (1936, 1937) and Rowan (1938). The number of comprehensive reviews of the subject of environmental control over pituitary activity, by these and other authors makes it unnecessary to include here more than a brief summary. In many birds successively additive or subtractive amounts of daylight or of wakefulness have been found to influence the activity of the pituitary and its secondary organs. On the other hand, this procedure is not effective in all birds tested, such as tropical birds, living in an environment in which the length of the day is fairly constant. This suggests that the method of hypophyseal control evolved may vary, even within smaller taxonomic groups. Certain fish (Stickleback) can be made to breed out of season by raises in temperature and will not respond in the light-ration experiment (Craig-Bennet, 1930), although this claim has been criticized (Tinbergen in Rowan, 1938). Other fish (trout) do respond in light-ration experiments (Hoover and Hubbard, 1937). It has been suggested that temperature changes are not regular enough to be suitable in guiding the breeding behavior of freshwater fish, but the high specific heat of water and the tremendous volume of the sea make temperature changes in the ocean regular enough to be useful to marine animals. These factors, light duration, wakefulness, and temperature, are manifestly of the greatest importance in those instances in which they are operative, but no doubt there are other avenues of nervous stimulation of the pituitary, e. g., copulation in the cat and rabbit, and the visual stimulation provided by the presence of eggs in the sparrow's nest. These facts do not as yet offer any means for a better understanding of the mammalian oestrous cycle, but do represent an advance in our knowledge of pituitary physiology. Through such factors as have been discussed, evolution has involved the pituitary in such spectacular phenomena as migration of entire populations of birds and fishes.

*Species differences in hypophyseal hormones*

Much of the exploratory work in lower vertebrates has been discouraging because the results of hormone injection have not been clear-cut, or because of the relatively massive dosages required to yield a minimum response. Because of this relative inefficiency of mammalian pituitary preparations in many lower vertebrates some workers have suggested that a pituitary hormone species-specificity might exist. Other workers, having found a lower vertebrate species which will respond to large doses of mammalian pituitary, make the opposite claim. This problem is of primary importance in the interpretation of bioassay values when the pituitary donor and the test animal are of widely divergent taxonomic types. For example, under favorable conditions the salamander

*Triturus pyrrhogaster* can be made to ovulate with a minimum dose of 200 rat units of sheep pituitary gonadotropic extract. Two or three frog pituitaries (*Rana pipiens*) will produce the same effect. According to the usual practice of equating rat, rabbit, bird, and other units, one frog pituitary would be equivalent to about 100 rat units of mammalian gonadotropic substance. But we know that this is not true from the work of Adams and Granger (1938) who found that 211 *Rana pipiens* pituitaries are needed to elicit even slight ovarian stimulation in an immature mouse. It may be well to regard the species factor seriously even when dealing with different mammalian hormones in mammalian test animals. In evaluation of this loss in efficiency of a pituitary hormone when administered to animals having more and more remote relation to the donor species Creaser and Gorbman (1936, 1939) and Benazzi (1939) have referred to a "relative species specificity." It is not difficult to find a probable physical basis for this phenomenon when it is remembered that the pituitary hormones have been shown to be protein in nature. It is well known that corresponding proteins vary sufficiently, even between closely related species, to make possible detection of their variation by immunological methods. Of the pituitary hormones, the lactogenic has recently become isolated as a pure protein. Using such preparations of lactogenic hormone from sheep and beef pituitaries, Li, Lyons, and Evans (1940, 1941) have been able to demonstrate an actual difference in solubility and in content of the amino acid tyrosine, even between these relatively closely related ungulates. Conceivably, the opportunities for protein hormone variation between widely divergent taxonomic groups have been many, and the change in the hormone can finally become great enough to become detectable physiologically in hormone exchanges between species.

SUMMARY

The most primitive living vertebrates already possess a fully differentiated pituitary body. The evolutionary antecedents of the pituitary body are unknown, and it does not seem probable that they shall ever be found.

Within the vertebrate group the structural relationships of the parts of the pituitary are fairly constant. The most remarkable variations are the presence of a "ventral" lobe in elasmobranchs, the presence of an *Übergangsteil* in teleosts, and the absence of the pars intermedia in birds and some mammals.

Exploration and comparison of the hormone content of pituitaries of lower vertebrates with mammals is still far from complete, but several interesting conditions have been shown to exist. The presence of the luteinising hormone has been claimed for the hypophyses of fish and birds, neither of which has corpora lutea. The lactogenic hormone has been reported in all vertebrate classes, but its "target organ" is found only in one.

Environmental factors influencing cyclical activity of the pituitary may be of a different nature even within rather closely related vertebrate groupings.

The reduced efficiency of administered pituitary hormones from very divergent species may be explained by the concept of a "relative species-specificity."

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# OBSERVATIONS AND EXPERIMENTS ON MATING BEHAVIOR IN FEMALE MAMMALS (*Concluded*)

By WILLIAM C. YOUNG
*Yale Laboratories of Primate Biology*

## FACTORS INVOLVED IN THE INDUCTION OF MATING BEHAVIOR AND IN THE REGULATION OF ITS CHARACTER

THE induction of mating behavior in female mammals is the result of very complex processes. The interaction of endocrine, neural, genetic, ontogenetic, nutritional, environmental, psychological, pathological and age factors is known to be involved and doubtless others are important. Because of this complex background, the part played by each factor is difficult to determine. In the normal animal a given combination of ovarian hormones may induce heat, but their production depends on an interplay of extrinsic and intrinsic factors and the character of the response they elicit may be determined by the reactivity of the soma they stimulate and the elements of the external situation in which the animal is living. Nevertheless, in any discussion of the subject, some starting point must be chosen. In what follows the ovarian hormones have been selected, not because they are necessarily the exclusive limiting factor, but because they are the means to the induction of heat by experimental procedures and the means by which the rôle of the other factors can be elucidated.

### *Ovarian hormones*

The factors immediately responsible for the display of the estrous responses have long been known to be ovarian in origin because complete ovariectomy is invariably followed by a cessation of cyclic reproductive activity. The willingness of rabbits to copulate within 48 hours after ovariectomy (Hammond and Marshall, 25; Reynolds, 31) and the display of heat recorded for the rat on the first day after the operation (Hemmingsen, 33) do not militate against this generalization. Post-operative heat, when it occurred, probably can be accounted for by the supposition that the animals were in heat at the time of the operation or that the operation was performed shortly before heat but after the effective stimulus had begun to operate. Nor does Robson's (38) report of a spayed *Macacus rhesus* monkey which permitted copulation discount the importance of the ovary. In mature monkeys, as in man, psychological factors may influence a situation which in lower mammals is under rigid hormonal control.

The identity of the hormones which induce normal heat responses in the rat and guinea pig became apparent only gradually. Those responsible for estrus in the other laboratory mammals and in wild species are not yet known with certainty. The first adequately controlled experiments were those of Allen (23), Allen and Doisy (23) and Allen, Francis, Robertson, Colgate, Johnston, Doisy, Kountz and Gibson (24) on spayed mice

and rats. Following the injection of follicular fluid extracts into 11 animals which were observed for evidences of mating, the indication of coitus in 7 (2 rats and 5 mice) was taken as evidence for the conclusion that estrous instincts are stimulated by the action of the follicular fluid hormone named "oestrin" by Parkes (29). Discounting the numerous experiments in which the observations were limited to the vaginal condition, what were regarded as confirmatory results were later obtained by Bourg (31), Hemmingsen (33), Kun (35) and Ball (36a). The irregularity with which mating responses were induced by injections of estrin was generally noted (Parkes, Fielding and Brambell, 27; Hemmingsen, 29, 33; Marrian and Parkes, 30; Wiesner and Mirskaia, 30), but was attributed to a postulated high threshold for mating (Marrian and Parkes, 30; Wiesner and Mirskaia, 30).

Although numerous investigators had postulated that the action of an additional factor might be involved (Asdell and Marshall, 27; Frei and Lutz, 29; Parkes, 29; Wiesner and Mirskaia, 30; Grant, 34; Witschi and Pfeiffer, 35; and Young, Dempsey and Myers, 35a), the suggestion was not considered seriously until Dempsey, Hertz and Young (36) showed that the induction of heat with any degree of regularity in the guinea pig depends on the synergistic action of estrogen and progesterone. Furthermore, when estrogen is followed by progesterone, large quantities of the former hormone are not necessary except in the few animals which are relatively insensitive to the conditioning action of estrogen (Boling, Young and Dempsey, 38). Recently estrogen and progesterone given in sequence to the rat have been found to be more effective than estrogen alone (Boling and Blandau, 39; Boling, Blandau, Rundlett, and Young, 41). Ball (39), injecting the two hormones somewhat differently, did not have the same degree of success with rats of the strain she used.

When the results from the experiments by Dempsey, Hertz and Young were first announced, doubt was expressed that progesterone is produced prior to ovulation which is when heat begins, but the luteinization of cells of the theca interna and stratum granulosum as early as the first day of heat in the mare (Seaborn, 25), the cessation of uterine motility between the 5th and 8th hour after copulation in the rabbit (Reynolds and Friedman, 30; Reynolds and Allen, 32), the positive Bitterling ovipositor test for progesterone given by follicular fluid from the sow and cow (Duyvené de Wit, 38), and the decrease in water content of the rat's uterus prior to ovulation (Astwood, 39) attest to the probability of its presence in the unruptured follicle.

The suggestion was also made that a supplementary injection of estrogen might be as effective as progesterone, but thus far only negative results have followed this procedure in the guinea pig (unpublished data) and in the rat (Boling and Blandau, 39).

If the observations summarized above may be assumed to be conclusive, heat in the normal female guinea pig and rat is stimulated by the conditioning action of estrogen followed by the secondary action of progesterone produced in the maturing follicle. Following tests of 7 closely related compounds, Hertz, Meyer and Spielman (37) reported that in this respect the action of progesterone is specific. Since then, however, Soderwall (40) has found that pregneninolone given orally is effective, van Heuverswyn, Collins, Williams and Gardner (39) have reported that desoxycorticosterone acetate will also induce heat following a conditioning

injection of estrogen, and Torstveit and Mellish (41) state that adrenal cortical extracts act similarly. In their animals, the interval between the injection of the desoxycorticosterone acetate and the beginning of heat is longer than that worked out by Collins, Boling, Dempsey and Young (38).

The estrogen conditioning action is not limited to any one compound. Although no systematic investigation has been made, several substances which are known to induce vaginal cornification have also been found to be estrogenic in the sense that they induce the mating responses alone or in combination with progesterone when injected into spayed animals. In the work on the rat and guinea pig done by Blandau, Boling, Collins, Dempsey, Hertz and Young, estrone and estradiol benzoate were used. Success has also been reported following the injection of estriol and 9:10-dihydroxy-9:10-di-n-propyl-9:10-dihydro-1:2:5:6-dibenzanthracene into rats (Hemmingsen and Krarup, 37a), triphenyl ethylene into mice, hypophysectomized rabbits (Robson and Schönberg, 37) and a dog (Robson, 38), and stilbestrol di-ethyl into rats (Dodds, Lawson and Noble, 38) and guinea pigs (Leighty and Wick, 39; Leighty, Wick and Jeffries, 41).

In any theory of the hormonal factors involved in the induction of heat in the guinea pig and rat allowance must be made for the effective action of estrogens in many animals. There is no question but that large quantities of estrogen stimulate mating responses in a large percentage of individuals. Indeed Stone and Gibb (41) have recently induced estrus in all of fifteen rats by an initial injection of 1000 I.U. Theelin followed by 666 I.U. daily. Two questions, however, are critical: Do animals which fail to respond to the largest quantities of estrogen display estrous reactions when they are injected with the two hormones? When an estrogen induced heat is shown, is it strictly comparable with the heat displayed by normal animals and with the estrogen-progesterone induced heat in spayed animals? Guinea pigs and rats that were refractory to estrogen alone responded to supplementary injections of progesterone in the experiments by Dempsey, Hertz and Young (36), Boling and Blandau (39) and Boling, Blandau, Rundlett and Young (41). Ball (39) has not had the same success, but her procedure was different. The second question has received some attention for the guinea pig (Boling, Young and Dempsey, 38) and rat (Boling and Blandau, 39). In both species the estrogen- and the estrogen-progesterone-induced heat differ in at least two details. The estrogen-induced heat does not always rise at once to its greatest intensity and then taper off gradually to the non-estrous state, and it tends to be longer.

The results suggest that in the guinea pig and rat, by some mechanism which is completely obscure, the estrogens are very nearly able to stimulate normal heat responses, but for some reason they fall short, and that progesterone, likewise by means of a mechanism of which we have no knowledge, has a supplementary rôle on which the appearance of normal heat responses depend.

Indications are that both individual and species differences exist with respect to the extent estrogens are effective. Adult guinea pigs have been encountered in which heat did not occur prior to ovariectomy, but after ovariectomy it was induced when twice the usual conditioning quantity of estrogen was injected (Boling, Young and Dempsey, 38). Before their ovaries were removed these animals showed normal vaginal changes and probably would have

been capable of normal reproduction if properly timed artificial insemination had been made (Soderwall and Young, 40), but as far as the stimulation of mating activity is concerned, they are assumed to have been relatively insensitive to the conditioning action of estrogen. Individual differences in sensitivity to estrogens have also been found in rats (Hemmingsen, 33; Hemmingsen and Krarup, 37a; Boling and Blandau, 39; Boling, Blandau, Rundlett and Young, 41).

The existence of species differences is suggested by a comparison of data obtained from the rat and guinea pig. The percentage of rats which responded to given quantities of estrogen was higher than the percentage of guinea pigs which responded to comparable quantities (Boling and Blandau, 39; Dempsey, Hertz and Young, 36). Furthermore, untreated rats in which the luteinizing action was insufficient to cause ovulation have been found in heat (Boling, Blandau, Soderwall and Young, 41), whereas in the untreated guinea pig heat without ovulation has not been encountered (Young, Dempsey, Myers and Hagquist, 38).

Since the species which have been investigated show differences in their sensitivity to estrogens, it is reasonable to expect that the range of variation will be found to be great when additional species are studied. In fact, many may be encountered in which the mating responses are normally induced by estrogens alone. The possibility is suggested by three groups of observations.

The first is that estrogens alone have been sufficient to induce heat in spayed rabbits (Lacassagne and Gricouroff, 25; Büttner and Wienert, 35), spayed and anestrous sheep (Cole and Miller, 35; McKenzie and Terrill, 37), spayed mares (Neves e Castro, 38), spayed cats (Bard, 36, 39; Maes, 39, 40b), spayed and anestrous dogs (Kunde, D'Amour, Carlson and Gustavson, 30; Robson and Henderson, 36; Leathem, 38; Robson, 38; Sammartino and Arenas, 39), and spayed monkeys (Ball, 36b; Hartman, 38). To be sure, the quantity of injected estrogen was usually large and the results frequently irregular. Consequently, the rôle of progesterone cannot be excluded until the action of smaller quantities of estrogen followed by progesterone has been tested.

The possibility that estrogen alone is sufficient to induce heat in some species is suggested, secondly, by the fact that, following the injection of gonadotrophic hormones extracted from human menopausal or pregnancy urine, mating responses have been displayed by dogs before there is any visible evidence of luteinization (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leathem, 38; Leathem and Morrell, 39). Here again, though, judgment must be withheld until it is known that follicular fluid in follicles at the stage of development when estrus begins contains only estrogen. Morphological evidence for the presence of progesterone in such follicles in the rabbit, guinea pig, rat, cow, and sow is absent; nevertheless physiological evidence suggesting that it is present has been cited.

A third group of observations is perhaps most convincing that in some species estrogen is sufficient for the induction of mating responses. In the cat, rabbit and ferret, and occasionally in the mare, heat is displayed prior to the time of the preovulatory swelling and therefore before the follicles are suspected of having any progesterone content. In certain bats the follicles which are present at the time of the autumnal heat are even less developed. According to Courrier (22) they do not contain follicular fluid and according to Guthrie (33) and Guthrie and Jeffers (38), the follicle which is respon-

sible for the heat induced in the fall has only a small antrum and is not even intermediate in size. As before, however, such morphological studies are not sufficient to give finality to the conclusion they suggest. Until the hormonal output of the ovaries at the time of heat is known, and until replacement therapies have been attempted in spayed individuals, decision must be withheld.

Not all the attempts to induce estrous behavior artificially have involved injections of ovarian hormones into spayed animals. Following the discovery of the importance of the gonadotrophic hormones for ovarian function by Smith and Engle, and Zondek and Aschheim (Smith, 39; Fevold, 39; Engle, 39), numerous tests of their morphological and physiological action on intact animals were accompanied by observations of mating behavior. Data bearing on the action of these hormones have been accumulated for prepuberal rats (Mahnert, 30; Cole, 36, 37), constant estrous rats (Witschi and Pfeiffer, 35; Ball, 36a), hypophysectomized rats (Evans, Meyer and Simpson, 33; Liu and Noble, 39), prepuberal mice (Mirskaya and Crew, 30; Wiesner and Mirskaia, 30), diestrous guinea pigs (Dempsey, Hertz and Young, 36), prepuberal rabbits (Mahnert, 30), anestrous sheep (Cole and Miller, 33, 35; McKenzie and Terrill, 37), normal mares (Catchpole, 35; Zavadowsky and Goldberg, 37; Neves e Castro, 38), anestrous ferrets (Hill and Parks, 30), anestrous and metestrous dogs (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leathem, 38; Leathem and Morrell, 38, 39), and anestrous cats (Friedgood, 39; Windle, 39). In general, the expectation that these substances injected into prepuberal, anestrous, diestrous or hypophysectomized individuals would induce mating responses through their action on the ovaries, has been realized. In certain experiments the percentage of animals in which heat was induced was small (Hill and Parkes, 30; Mahnert, 30; Mirskaya and Crew, 30; Wiesner and Mirskaia, 30; McKenzie and Terrill, 37). In at least two experiments the period of heat was considerably shorter than that displayed normally (McKenzie and Terrill, 37; Dempsey, Hertz and Young, 36). Such irregularities indicate that the optimal dosage and method of administration were not always found. On the other hand, results with the dog were more successful in that the experimentally induced heat periods were similar to those seen in normal estrous animals. Such being the case, the gonadotrophic hormones must have been administered in such a way that their normal manner of action on the ovaries was approximated.

From an economic standpoint this method of inducing heat may be of considerable value. As a means to a better understanding of the factors which are responsible for the induction of heat, it will be of greater value when the precise part played by each gonadotrophic hormone in producing the ovarian hormones is known. So long as the injection of an apparently pure follicle-stimulating substance is sometimes followed by luteinization (Foster and Fevold, 38; Saunders and Cole, 38), and the injection of the luteinizing fraction is sometimes followed by follicular growth (Leathem and Morrell, 39), the administration of these hormones to intact animals does not give as reliable an indication of the hormones directly involved in the induction of heat as the administration of purified ovarian hormones to spayed animals.

### *Other endocrine factors*

There is no evidence that endocrine organs other than the ovaries have any direct rôle in the induction of estrus. A

sufficiently high percentage of hypophysectomized animals have mated following the administration of estrogenic substances to exclude the possibility that secretions of this gland are necessary beyond their action as gonadotrophic agents. Robson and Schönberg (37) report that two hypophysectomized rabbits injected with triphenyl ethylene mated, and according to Sammartino and Arenas (39), hypophysectomized spayed dogs displayed the behavior of heat after being injected with 200 I.U. or more estradiol benzoate for 15 to 87 days. Maes (40a) was quite successful with hypophysectomized cats, 7 of 8 responding to 10,000 I.U. estradiol benzoate after an interval of 2 to 5 days. Early attempts to induce heat in hypophysectomized rats failed (Ball, 36a), but results reported more recently were positive (Ball, 41). Dempsey (39) did not obtain any response following the injection of estrogen and progesterone into 7 hypophysectomized guinea pigs, although 3 spayed animals from which the hypophysis had not been completely removed responded normally. The reviewer attributes Dempsey's failure to the severe general effects of this operation on the guinea pig rather than to the possibility that the action of estrogen and progesterone must be supplemented by some secretion from the pituitary.

Although the direct participation of hypophyseal hormones in the induction of estrus seems unlikely, a certain regulatory action on the length of heat is indicated by data obtained from a variety of species. In the guinea pig (Young, Dempsey, Myers and Hagquist, 38), the ewe (Quinlan and Maré, 31), the cow (Williams and Williams, 21), the mare Schtschjekin, 30; Hammond, 34; Mirskaia, 35; McKenzie and Andrews, 37; Neves e Castro, 38; Day, 39b, 40), the cat (Liche, 39), and the ferret (Marshall, 04a, 04b; Robinson, 18; Hammond and Marshall, 30), the length of heat seems determined in part by the time required for ovulation to occur. Since structural conditions in the ovaries of guinea pigs which were examined could be excluded from having such an effect, the manner of hypophyseal action resulting in ovulation has been postulated to be important (Young, Dempsey, Myers and Hagquist, 38). Obviously this statement leaves much to be explained and proved, but in the opinion of the reviewer it indicates another direction toward which we must look for the identification of the factors which determine the character of heat.

The effects of adrenalectomy and thyroidectomy on the vaginal condition or activity have received some attention, but the rôle of these and the other glands of internal secretion on the induction of mating responses has been but little studdied. It is only known that adrenalectomized female rats which ultimately died of adrenal insufficiency mated soon after the operation (Tobin, 40). With norms of behavior now established for the rat and guinea pig (Hemmingsen, 33; Ball, 37a; Blandau, Boling and Young, 41; Young, Dempsey and Myers, 35b; Young, Dempsey, Myers and Hagquist, 38; Young, Dempsey, Hagquist and Boling, 39), a more comprehensive investigation of the relationship between these important endocrines and mating behavior would be of interest.

### *The ovarian condition*

Only when abnormalities exist which interfere with the regularity of follicle growth or ovulation, or when abnormalities occur as a consequence of defective hypophyseal function, does there seem to be an effect on mating behavior. The injuries caused by X-irradiation (Parkes, 26, 27a; Genther, 31, 34) or traumatiza-

tion (Wang and Guttmacher, 27; Ball, 34b; Lipschütz, 37, 38) are abnormalities of the first type. In Parkes' and Genther's experiments heat was displayed by many animals, but despite the implication given by Parkes (27b) that essentially normal cycles occurred, the reviewer feels that irregularities were shown in the length of heat and cycle which represent an effect of ovarian injury.

The failure of ovulation and development of persistent cystic follicles is an abnormality of the second type. In the lower mammals this condition has been described for the rat (Hemmingsen and Krarup, 37b), guinea pig (Courrier, 25) rabbit (Harris, 37), ewe (Grant, 34), cow (Pearl and Surface, 15; Williams and Williams, 21) and horse (Williams and Williams, 21). It is said to be responsible for nymphomania and even the assumption of secondary male sex characters in the cow, for nymphomania in the rabbit and horse, to result in constant estrus in the rat—a state which the reviewer assumes is analogous with the nymphomanic condition of cows and horses, and to be without effect in the ewe. The behavior of the guinea pig studied by Courrier (25) was not observed, but the prolonged, intermittent estrus in this species (Young, Dempsey, Myers and Hagquist, 38) is thought attributable to a delay in ovulation, and to represent an approach to constant estrus.

In other respects, the ovarian condition apparently can vary within rather broad limits without influencing the cyclic appearance or character of heat. In sheep (Marshall, 04a, McKenzie and Terrill, 37) and guinea pigs (Young, Dempsey, Myers and Hagquist, 38) no relationship exists between the number of maturing follicles and the length of heat, provided one ruptures. The length of heat is likewise not affected in guinea pigs by variations in the extent of general follicular development, provided some growing follicles are present, or in the extent of rete cyst formation, provided some ovarian parenchyma is present. In the rabbit no close relationship exists between the number and size of follicles and estrus. Büttner and Wienert (35) have observed animals which refuse the buck continuously when many large, intact follicles are present and others which accept the buck immediately and ovulate easily when only a few are present.

No ovarian condition has been found which could account for the mounting activity which is displayed by the rat (Beach, 38b). In the guinea pig no relationship exists between the extent of general follicular development or rete cyst size and the frequency of mounting. The average number of ruptured follicles was higher in animals in which mounting activity was greatest, but the significance of this observation has yet to be explained (Young, Dempsey, Myers and Hagquist, 38). The prolonged periods of mounting activity displayed by nymphomanic cows are assumed to be a normal accompaniment of the prolonged heat and not to be attributable to any special secretions of the cystic follicles. For mounting activity as for heat the conclusion reached by Young, Dempsey, Myers and Hagquist seems valid. "... the ovary is largely an intermediary, on the one hand responding to and reflecting the character of stimuli from the hypophysis, and on the other, possessing a potentiality of action which is limited by the responsiveness of the soma upon which its secretions act."

### *Neural factors*

Participation of the nervous system in the induction and display of mating behavior has long been assumed. Indirect evidence was given by observations on the

close relationship between seasonal changes in the daylight ration and reproductive activity (Baker and Ranson, 32; Bissonnette, 32; Bissonnette and Csech, 37; Whitaker, 36) and on the close relationship between the approach of darkness and the onset of heat (Dempsey, Myers, Young and Jennison, 34; Browman, 37; Hemmingsen and Krarup, 37b; Beach, 38a). Dependence on the nervous pathways for conduction of the light stimulus, is indicated by the delay or failure in the appearance of heat following transection of the optic nerves in ferrets (Clark, McKeown and Zuckerman, 39). Other indirect evidence for nervous system participation in the control of heat is adduced from the action of copulation in shortening heat in the rabbit, cat and ferret.

Direct evidence that nervous centers mediate the estrous responses has only recently been given (Bard, 35, 39; Brooks, 37; Fisher, Magoun and Ranson, 38; Dempsey and Rioch, 39; Dey, Fisher, Berry and Ranson, 40; Brookhart, Dey and Ranson, 40, 41). It had previously been shown that heat periods recur in the dog following transection of the cord craniad to the spinal origin of the sympathetic nervous system (Sherrington, 06), in the rabbit following complete removal of the sympathetic chains (Brooks, 38), in abdominally sympathectomized rats Bacq, 32a, 32b), and in partially and totally sympathectomized cats (Bard, 35; Simeone and Ross, 38). Typical heat behavior was displayed by a cat during spontaneous estrus and by spayed, estrogen-injected cats after complete removal of the neocortex together with part of the rhinencephalus, a little of the striatum and the rostrolateral half of each thalamus (Bard, 34, 36, 39, 40; Bard and Rioch, 37). The after-reactions of these animals though distinct and sometimes briefly frantic, were usually delayed and lacked the vigor and nicety of execution which characterized them before the cerebral ablation (Bard, 39, 40). Destruction of the cortical area did not prevent mating in the rat (Stone, 38; Davis, 39). A cat in which the thalamus was removed bilaterally showed mating behavior, copulated and became pregnant (Dempsey and Morison, personal communication). According to Ranson (34) mating occurs in female cats with bilaterally symmetrical lesions in the tuber cinereum, lateral to or behind the infundibulum. Magoun and Bard have had several cats with somewhat comparable lesions whose responses were the same as before operation, but the marked reduction in the capacity of one of these animals to exhibit estrual behavior prompts Bard (40) to suggest that the possibility of hypothalamic involvement has not been excluded. In the rabbit estrous behavior was not abolished by concurrent destruction of the auditory and visual end-organs, removal of the olfactory bulbs and bilateral ablation of the neocortex (Brooks, 37) or by complete section of the pituitary stalk (Brooks, 38). In neither the cat nor the rabbit did denervation of the vagina and vulval region have any effect. Therefore afferent impulses from the genitalia are not involved in the induction of heat in these species (Bard, 35, 39; Brooks, 37).

In the guinea pig bilateral ablation of the neocortex and other portions of the forebrain was without effect except that the responses were more easily fatigued, possibly due to non-specific effects of the operation. Likewise, heat responses were induced in an animal following transection of the brain-stem immediately anterior to the mammillary bodies, but when a second cut was made just anterior to the superior colliculus and just behind the mammillary bodies, no further responses were shown (Dempsey and Rioch, 39).

Similar results were obtained on a cat. In the same experiments Dempsey and Rioch showed that estrual behavior can also be abolished in the guinea pig by destruction of an afferent pathway for the reflex responses which runs through the posterior quadrants of the cord, crosses in the medulla and runs through the tectum mesencephali. The experiments taken together are considered to offer circumstantial evidence that estrous behavior results from the action of the sex hormones on the central nervous system and that the anterior limit of this neural mechanism lies between the intercollicular level and the anterior limit of the mammillary bodies. Bard (40), on the other hand, induced heat in a cat after complete bilateral destruction of the posterior hypothalamus, and believes therefore that the essential region for sexual behavior lies further back in the mesencephalon. Fisher, Magoun and Ranson found that cats did not mate after destruction of the supraoptic region, and Dey, Fisher, Berry and Ranson (40) report similar results from the guinea pig. The sterility in guinea pigs with anterior hypothalamic lesions is not a result of failure of the ovaries to produce sex hormones because the animals showed cyclic cornification and failed to mate following injections of estrin and progesterone (Brookhart, Dey and Ranson, 40, 41). Nevertheless, the view that the anterior hypothalamus is the region necessary for sex behavior fails to account for the presence of heat in the guinea pig after removal of all tissue rostral to the mammillary bodies (Dempsey and Rioch, 39) and for the occurrence of estrus in Bard's cat whose lesion destroyed not only the entire posterior hypothalamus, but all of the descending hypothalamic connections as well. Additional experiments are in progress and it is probable that these conflicting opinions will soon be resolved.

The results from a study by Maes (39, 40b) suggested a conclusion which is considerably different from those given above. Following transection of the cord at the level of the first cervical segment in eight normal estrous cats and in two spayed cats brought into heat by injection of estradiol, all except one displayed raising of the pelvis, treading and movements of the tail when tapped on the perineum. Two of the three uninjected spayed animals showed some raising of the pelvis. He concludes:

> These experiments demonstrate that some components at least of the sexual behavior are short arc reflexes, comparable to the scratch-reflex, which can be elicited independently of the higher centers, but the occurrence of which depends strictly on hormonal conditions. It seems, therefore, that the existence of a hypothetical sexual center should be accepted with caution, and then not so much as a pace-maker under the influence of which unspecific activities of the spinal cord are transformed into specific sexual reactions, than as a mechanism coordinating certain independent activities pre-existing at different levels of the brain stem.

That part of Maes' conclusion in which he emphasizes the dependence of hormonal stimulation is questioned because of the response given by two of his uninjected spayed animals. Furthermore, similar responses have been obtained from ovariectomized female cats decapitated when completely anestrous and from decapitate males (Bromiley and Bard, 40; Bard, 40).

In normal animals the neural paths to the pituitary may be involved at least secondarily. In the rat they mediate certain environmental effects such as cold on the cycle (Uotila, 40; Dempsey and Uotila, 40). Following pituitary stalk section many, but not all guinea pigs and rats become acyclic (Dempsey, personal communication).

An interesting point is brought out by

Dempsey and Rioch (39) and Dempsey (39). When animals are not in heat, evading reactions are shown to the same stimuli which evoke sexual behavior when animals are in heat. Inasmuch as both responses are lost with the same lesions of the colliculi and cord, it is possible that the same centers and pathways are involved.

Beyond these efforts to identify centers and tracts which mediate mating responses little has been done. The rôle of the hormones and the nature and manner of their action on the nervous system are unknown. For species in which mating behavior is induced by the synergistic action of estrogen and progesterone, no one has suggested what the nature of the conditioning action of estrogen and the supplementary action of progesterone might be. It is not certain that all the heat responses are controlled by the same nervous mechanism. Data have been presented which suggest that in the guinea pig one mechanism may control lordosis and the willingness to mate and another the homosexual or mounting activity (Young and Rundlett, 39). Finally, it is clear from data which are presented in the following section that some individuals are more sensitive to hormones than others and that certain changes in sensitivity occur as an animal develops. It should be ascertained if this sensitivity which is so important for the character of mating behavior is, among other possibilities, an expression of the responsiveness of the neural centers to hormone action.

### *Sensitivity to estrogen-action*

Numerous observations indicate that animals differ greatly in their sensitivity to estrogen-action and whether heat is induced by estrogen alone or by the synergistic action of estrogen and progesterone, these differences account for many of the variations displayed by normal animals and by animals following replacement therapies. This possibility was first emphasized by investigators who were depending on vaginal smears for estrogen-assays (Coward and Burn, 27; Kahnt and Doisy, 28; Marrian and Parkes, 29b; D'Amour and Gustavson, 30). Of those who have investigated mating behavior, Wiesner and Mirskaia (30) seem to have been among the first, if not the first, to suggest that individual differences in the estrogen threshold might be important for the induction of mating responses. Since then the existence of spayed rats and guinea pigs whose threshold to estrogens does much to determine the response which may be expected, has been noted by Hemmingsen (33), Hemmingsen and Krarup (37a), Boling, Young and Dempsey (38), Boling and Blandau (39) and Boling, Blandau, Rundlett and Young (41).

Of immediate interest are the factors to which differences in sensitivity to estrogens can be attributed. Seasonal influences must be considered, but the little information which exists is difficult to evaluate. Bard (40) appears to assume that a seasonal refractoriness exists to estrogenic stimulation. Cole and Miller (35), on the other hand, induced heat in anestrous ewes with a single injection of estrogen and concluded that the absence of sexual desire during the anestrum is attributable to an insufficiency of estrogen. Results from injection of animals, spayed during the breeding season, which would have served as controls are not reported. By means of injections of pregnancy urine extracts (Hill and Parkes, 30) and increased daily light ratios (Bissonnette, 32), anestrous ferrets have been induced to mate. The latter treatment has also been effective on the deer mouse (Whit-

aker, 36), and the raccoon (Bissonnette and Csech, 37). For the problem at hand, such experiments indicate only that anestrous animals can respond to heat inducing stimuli. Quantitative data which would be of value in determining whether or not the sensitivity to estrogens varies from season to season can be obtained only by injecting estrogens into these species during the anestrum.

More suggestive of possible seasonal variations in the sensitivity to estrogens are observations on the bank vole (Brambell and Rowlands, 36). At the beginning of the breeding season the majority of older females experience a number of sterile cycles. Ovulation is known to occur, but there is no evidence that it is accompanied by heat. By contrast younger animals which attain puberty during the latter part of the season, frequently become pregnant at the time of the first ovulation. What is involved can only be conjectured, but on the surface a seasonal factor which influences the sensitivity of the animals to the ovarian secretions is suggested.

On the basis of mating behavior responses (Ball, 36b) and the uterine response to injected estrogens (Zuckerman, 37, 38), cyclic changes in sensitivity to estrogen-action are suggested as occurring in spayed monkeys. Inherent rhythms which are independent of ovarian action have also been postulated as being shown by the rat (Kostitch and Télébakovitch, 28; del Castillo and Calatroni, 30) and guinea pig (Dempsey, 37). Consequently, the possibility that such rhythms may be associated with changes in sensitivity to estrogen must be considered. On the other hand, the consistency with which guinea pigs displayed mounting activity following repeated injections of estrogen and progesterone over a period of more than a year does not suggest any conspicuous cyclic variation in the sensitivity to estrogen in this species (Young and Rundlett, 39).

Nutritional deficiencies are naturally thought of in an enumeration of the factors which modify the sensitivity to estrogen-action, especially as the lack of specific dietary requirements and undernutrition are debilitating and terminate or modify cyclic reproductive activity. Unfortunately, there is no unequivocal evidence to indicate whether or not such a relationship exists. Rats maintained on a diet deficient in vitamin E come into heat, copulate and ovulate despite their inability to retain the fetuses during the entire gestation period (Evans and Bishop, 23; Evans and Burr, 27). In several investigations involving other dietary deficiencies interference with the pituitary gonadal mechanism is indicated by the abnormal ovarian condition (Loeb, 17; Evans and Bishop, 23), or by delays in and the termination of ovulation (Osborne, Mendel and Ferry, 17; Papanicolaou and Stockard, 20; Evans and Bishop, 22; Parkes, 28; Marrian and Parkes, 29a; Guilbert and Hart, 30; Quinlan and Maré, 31; Roux, 36), but the possibility that the estrogen threshold might also have been raised has not been tested.

Conflicting opinions exist with respect to the effect of "flushing" of ewes before the beginning of the reproductive season. Grant (34) believes that flushing hastens the onset of the breeding season, not by causing an earlier production of ripe follicles, but by intensifying the secretion of estrogen or possibly by increasing the sensitivity of the receptor mechanism on which this hormone acts. Marshall and Potts (24) and Clark (34), on the other hand, state that flushing does not bring ewes into heat earlier.

The only observations which provide any direct information about the effect

of the nutritional level on the character of heat are those by McKenzie and Terrill (37). Two groups of 20 ewes each were kept on different planes of nutrition for about four and a half months. Those on the high plane gained an average of 14 pounds, and those on the low plane lost an average of 10 pounds. Nevertheless, the duration of estrus did not vary, the mean length was 25.49 hours in the former group and 25.56 hours in the latter. It is assumed from this, that under the conditions of McKenzie and Terrill's experiment, no change occurred in sensitivity to estrogen-action.

The interval between injections is considered by some to influence the vaginal response to injected estrogens (Kahnt and Doisy, 28; D'Amour and Gustavson, 30), but the few data which have been obtained in studies of behavior indicate that in the spayed rat and guinea pig the sensitivity is as great several months after a series of injections as it is only a few days later (Hemmingsen, 33; Boling, Young and Dempsey, 38). The conclusion is consistent with the point noted below that normally produced ovarian estrogens do not increase an individual's sensitivity to these hormones.

A factor to which differences in the sensitivity to estrogens can certainly be related is the age of the animal. In general the sensitivity to estrogen-action increases during the prepuberal period and probably during the first cycles in the pubescent female. Thereafter it appears to remain fairly constant for a very considerable portion of the reproductive life, after which a slight decrease may be shown. This conclusion is supported by data from intact females of several species for which the length of heat at different ages and the number of rupturing follicles are known, and by data obtained following the injection of prepuberally spayed animals.

The heat period of the cow is slightly longer than that of the heifer (Hammond, 27). Grant (34) states that the ewes he observed varied widely in age, but none of the differences in the estrous cycle were correlated with age. McKenzie and Phillips (30) and McKenzie and Terrill (37), on the other hand, state that lambs have shorter estrous periods than older ewes, that there is no significant change between the second and eighth years of age, and that a slight decrease is shown by aged ewes. In mares 4 to 11 years, 12 to 17 years and 18 to 24 years of age the periods of heat averaged 4.38, 4.51 and 4.04 days, respectively (Constantinescu and Mauch, 36). In the guinea pig the first two heat periods tend to be shorter than those which follow. Thereafter, until about the 500th day, the average length remains approximately constant (Young, Dempsey, Myers and Hagquist, 38; Young, Dempsey, Hagquist and Boling, 39).

The ability of prepuberal animals to display mating behavior when properly stimulated is shown by the response of intact immature rats (Smith and Engle, 27; Mahnert, 30; Kraft, 32; Cole, 36, 37), mice (Smith and Engle, 27; Mirskaya and Crew, 30; Engle, 31), rabbits (Mahnert, 30), and dogs (Swingle, Parkins, Taylor, Hays and Morrell, 37; Leathem, 38) to gonadotropic hormones, and by the response of spayed immature guinea pigs to injected estrogens and progesterone (Boling, Blandau, Wilson and Young, 39). The latter authors have also described a heat-like response displayed by newborn female and male guinea pigs, but they were unable to reproduce it by hormone injections before the 20th day.

Some information has been obtained about the character of the induced heat

in prepuberal animals (Wilson and Young, 40). By the 20th day it can be induced regularly, although only when 20 R.U. estrogen are injected. Fourteen of 15 injected animals of this age displayed heat periods the length of which averaged 6.3 hours, range 1 to 11.5 hours. By the 30th day heat can be induced by injections of 10 R.U. estrogen followed by 0.1 I.U. progesterone. Its length in 14 injected animals of this age averaged 7.3 hours, range 6 to 9 hours, which is slightly longer than but not significantly different from that in spayed mature females injected similarly (Collins, Boling, Dempsey and Young, 38). The results have been interpreted to indicate that the centers responsible for heat behavior in newborn females are relatively insensitive to estrogenic stimulation, but by the 30th day in most animals a nearly normal sensitivity has been acquired.

The influences which are responsible for these changes are unknown, but supplementary observations by Wilson and Young would seem to exclude the possibility that ovarian hormones are involved. The group of 30-day old guinea pigs referred to above, was spayed within 24 hours after birth. For comparison a group of 6 was spayed between the thirtieth and thirty-fourth day and then injected with 10 R.U. estrogen followed by 0.1 I.U. progesterone. The length of heat in the first group has been noted as averaging 7.3 hours, that in the second group averaged 6.3 hours, range 6 to 7 hours. When 24 months were allowed to elapse in another group of experimental animals, the result was the same. Heat was induced promptly and its length was not different from that in the controls. Obviously removal of the gonads at the time of birth does not retard the acquisition of a sensitivity to estrogen during the first 30 days of postnatal development or prevent retention of this sensitivity during at least a 24-month period.

When the idea of a priming action of estrogen at the time of the first heat was suggested (Young, Dempsey, Myers and Hagquist, 38), it was not suspected that the sensitivity to estrogens may develop independently. Either possibility, however, could explain the fact that the average length of initial heat periods tends to be less than that of those which occur subsequently, but the latter explanation is preferred.

Of the five factors mentioned above which conceivably could modify the sensitivity of animals to estrogenic substances, none can be held to account for the differences found in a colony of animals homogeneous with respect to age, season, availability of food and care, and yet it is under precisely these conditions that variations in threshold are shown. Apparently something more fundamental must be sought. This could be the action of one or more products of metabolism on the receptor tissues or an inherited quality of the soma. The former possibility is suggested by the observation that normal sensitivity to estrogens does not develop following the injection of androgens into female rats during the first 28 days of postnatal life (Wilson, Young and Hamilton, 40). More probable, however, is the likelihood that a genetic factor is involved. Genetic rather than gonadal factors have been postulated to have a dominant rôle in sexual differentiation during the prenatal and early postnatal periods of development (Wiesner, 34–35; Moore, 41; Wilson and Young, in press). That they may influence the sensitivity of the estrous behavior mechanism to estrogen is indicated by the experiments of Wilson and Young cited above, by Ball's (39) observation that male rats are more refractory to injected estrogens

than females, and by the failure of newly hatched female chicks and hens to display cock-like behavior when injected with testosterone propionate (Hamilton, 38; Hamilton and Golden, 39).

The extent to which sensitivity to estrogen-action is of importance for the problem of mating behavior in infrahuman primates does not seem to have been considered. It has recently been found that the quantity of urinary estrogens from a female chimpanzee which consistently avoids sexual contacts with males is as great as that from a normal animal studied simultaneously (Fish, Young and Dorfman, 41). Nevertheless, there is as yet no evidence that the failure of this female to mate is attributable to a low sensitivity to estrogens rather than to such non-sexual factors as social relationships or environmental circumstance. In a general way, however, differential sensitivity must exist among primates as well as among the lower mammals. If this much may be assumed, the problem is to ascertain when the failure to display sexual interest can be attributed to a low sensitivity to estrogens, when it can be attributed to social and other environmental factors, and whether or not the total picture ever involves both.

Closely related to the problem of estrogen-sensitivity is that of progesterone-sensitivity, particularly for species in which this hormone appears to be involved in the induction of mating behavior. The subject has been omitted, not because it is believed there is no variation in the threshold to this hormone, but because the possibility has received little if any attention.

### *Environmental influences*

The influence exerted by other animals on the character of the estrous responses is greatest among the infra-human primates. Among the lower mammals, the ability of a dominant male rat to succeed in copulation when a less aggressive animal would fail (Miller, 11; Stone, 22; Hemmingsen, 33; Ball, 37a) and the preference some ewes have for certain teasers (Roux, 36) have also been noted. On the whole, however, the character of the heat response is only slightly modified by the presence of other animals. Critical evidence that young, non-responsive mares are often brought into heat by placing them in a stall adjoining one containing a stallion or even with the male has not been found. The proximity of the bull to the cow is without stimulating action (Hammond, 27). Association with other animals, and especially those of the opposite sex, does not influence the time of sexual maturity or the normality of the first estrous responses in rats (Stone, 26) or guinea pigs (Ishii, 20; Louttit, 29). Physical maturation is of more importance for the development of reproductive behavior pattern than experience gained from association with other animals.

The character of the heat responses in domesticated and commonly used laboratory mammals is rarely influenced by handling. Wild species are entirely different. Many breed in captivity only after long periods of time and others have never been known to breed. Hartman's (23b; 39) observation that transfer of the opossum from the wild to the captive state frequently was followed by atresia of the ovarian follicles suggests that in such cases an interference with the pituitary gonadal mechanism is involved. With this much of a beginning already made, an experimental analysis of the problem would appear to be opportune.

When laboratory rodents are being handled, the behavior of the female is less easily disturbed than that of the male. In supervised breeding experiments or tests of behavior, Steinach (94) observed for the rat, Brooks (37) for the rabbit and

the reviewer for the guinea pig that copulation is usually accomplished more promptly if the female is placed with the male.

As a matter of convenience or for direct experimental purposes, reversal of the darkness-light relationship has been accomplished on the rat. Presumably heat is normal after the new rhythm is established (Hemmingsen and Krarup, 37b; Beach, 38a), although the occurrence of constant vaginal cornification in 2 of the 6 animals studied by Hemmingsen and Krarup (37b) suggests a disturbance which may be found to be reflected in the character of heat when more animals are studied. During conditions of constant darkness for a period of two months, heat ceased to be predominantly nocturnal in its occurrence in the guinea pig, but no effect was exerted on its character (Dempsey, Myers, Young and Jennison, 34).

## SUMMARY

The behavior displayed at the time of estrus is described for the female mammals for which data are sufficient to permit a characterization of the species. Reasonably comprehensive information exists for the rat, guinea pig and rabbit among the rodents; sheep, cattle, pigs and horses among the ungulates; the cat and dog among the carnivores; and the howler monkey, Rhesus monkey and chimpanzee among the infrahuman primates. The generalization is warranted that each species displays a characteristic pattern of behavior within the framework of which considerable individual variation is shown. This variation is greatest among the infrahuman primates, the circumstance being attributed to the greater plasticity of behavior in species at this phylogenetic level. In a very satisfactory number of species the behavior associated with estrus is easily identified and well adapted to investigation by quantitative methods.

In mammals which have been studied, estrous behavior has an endocrine basis. It is abolished by removal of the ovaries and restored by suitable replacement therapy. Little is known about the mechanism of hormone-action, but it appears to be mediated by a neural center or centers in the hypothalamus or even farther back in the mesencephalon. But much more is involved. Physiological factors in addition to those of endocrinal origin undoubtedly affect the character of estrus. Social and other environmental influences are assumed to be important, particularly in members of the higher Orders. Finally, individual differences that are a matter of age or differences that may be of genetic origin do much to determine the nature of the response which is shown. If any trend is evident beyond attempts to learn more about sex hormone action *per se*, it is an effort to ascertain more precisely the part played by these other factors.

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## LIST OF LITERATURE

In the text the first two digits have been omitted for the year of the reference, e.g., Cocks (1881) is shown as Cocks (81) and Aitken (1927) is shown as Aitken (27).

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# NUTRITION IN THE PROTOZOA

By W. H. JOHNSON

*Department of Biology, Stanford University*

AN UNDERSTANDING of the nutrition of an organism involves a knowledge of the specific substances needed and utilized by that organism in its metabolism and growth. In recent years tremendous advances have been made in the field of bacterial nutrition. Advances in protozoan nutrition have not been as rapid.

Protozoans obtain nourishment in different ways. Until recent years these were usually referred to as:

(1) holophytic nutrition—in which the organisms carry on photosynthesis and are capable of continued growth in a suitable inorganic medium, in the presence of light;
(2) saprozoic or saprophytic nutrition (also parasitic)—in which organic compounds in solution are required and utilized; and
(3) holozoic nutrition—in which the organisms ingest solid organic material. This ingestion of particulate matter, in contrast with the diffusive method of obtaining nutrient requirements as found in (1) and (2), is the characteristic animal-way of obtaining food.

When the various classes of the Protozoa are considered with respect to the mode or modes of obtaining nourishment, we find that:

(1) the three types of nutrition, holophytic, saprophytic and holozoic, occur in practically all the orders of the Mastigophora;
(2) holozoic nutrition is almost universal in the Sarcodina, saprophytism is rare;
(3) with the exception of certain highly modified parasitic forms, all of the Ciliata utilize solid food; and
(4) all of the Sporozoa exhibit parasitic nutrition.

Most of the colorless free-living protozoans exhibit, wholly or in part, holozoic nutrition. In this discussion a rather brief consideration of our knowledge of holophytic and saprophytic nutrition in the Protozoa is followed by a more detailed consideration of the problems of holozoic nutrition. Why a special interest in the nutrition of holozoic forms? The nutrition of any of these types is interesting from a physiological viewpoint. From a comparative physiological viewpoint the fact that less is known about the nutrition of holozoic forms than about either the holophytic or saprozoic forms suggests that more attention should be given to this type of nutrition. Knowledge gained about the nutrition of free-living holozoic forms, as well as about the other types, may be useful in gaining an understanding of the nutrition of related parasitic forms. The rôle of protozoans in the economy of the elements in nature is little understood and a solution of some of the problems of holozoic nutrition will aid materially in this field. There is a large group of biologists who consider that certain of these holozoic protozoans are especially suited for investigations on certain fundamental problems of protoplasm and of cells, problems of cell differentiation, of heredity, of sex and others, where completely controlled conditions, both en-

vironmental and organismic, are essential to final solutions. For these workers an exact knowledge of the nutrition of these forms is quite essential. And finally, there is an interest in the study of the nutrition of these forms because of the light which the information obtained may shed on evolutionary relationships. In this connection, Sandon (1932), in his monograph *The Food of the Protozoa*, p. 1, states,

> The animal kingdom presumably had its origin when some unicellular organisms, previously accustomed to nourishing themselves after the manner of plants, began to eat the bodies (either living or dead) of their neighbors. The rest of the story of the evolution of animals presents itself to us as something which follows with every appearance of inevitability and purposefulness out of this one revolutionary change. Though the earlier stages of this story may be irretrievably lost in the remote past, the unicellular organisms of the present day provide us with what we may reasonably imagine to be a very fair reconstruction of a very considerable part of it. Among the flagellates, organisms are still changing from plants into animals. Some of them can even be made to cross the boundary from one kingdom to the other under the carefully controlled conditions of a laboratory experiment. In many more cases the similarity between a colorless animal flagellate and another which contains chlorophyll is so close that the systematist includes them in the same family or even in the same genus, from which we conclude that the difference between them is a relatively recent development. From such beginnings the Protozoa—those unicellular creatures which have definitely adopted the animal way of living—show amazingly varied developments alike in morphology, in physiology and in ways of feeding. It seems hardly likely that these developments are not intimately connected with one another.

Researches of recent years by Lwoff, Dusi, Mainx, Pringsheim, Hall and others have shown that the nutrition of green forms formerly classed as holophytic or autotrophic varies, as also does the nutrition of those forms formerly classed as saprophytic or saprozoic. Hall (1939) has recently proposed a new classification of nutritional types based on the suggestions of several workers. He proposes to designate the holophytic type of nutrition as *phototrophic nutrition* with the following subdivisions on the basis of the simplest possible nitrogen requirements in each case:

(1) Photoautotrophic nutrition—characteristic of green forms which can grow in inorganic solutions, such as *Chlorogonium euchlorum*.
(2) Photomesotrophic nutrition—exhibited by green species which are able to grow in media containing amino acids but not in inorganic media, such as *Euglena dastes*.
(3) Photometatrophic nutrition—characteristic of green forms capable of growth in peptone solutions but not in amino acids or inorganic solutions, such as *Euglena pisciformis*.

For the colorless organisms which require an organic carbon source in the absence of chlorophyll, he proposes the term *heterotrophic nutrition*. On the basis of nitrogen requirements he divides heterotrophic nutrition into the following classes:—

(1) Heteroautotrophic nutrition—where there is the utilization of inorganic compounds of nitrogen in the presence of an organic carbon source, as in *Polytoma uvella*.
(2) Heteromesotrophic nutrition—in which the growth requirements may be satisfied by one or more amino acids as sources of nitrogen and of carbon (growth is usually more vigorous with an additional carbon source), as in *Polytomella caeca*.
(3) Heterometatrophic nutrition—characteristic of organisms which grow in peptone solutions but not in amino-acid media or in inorganic solutions, such as *Hyalogonium klebsii*.

A classic piece of work in the field of protozoan nutrition was that of Pringsheim (1921), who was perhaps the first to culture successfully a colorless flagellate in a sterile medium of known chemical composition. Working with *Polytoma uvella*, he found that this species could satisfactorily nourish itself with ammonium salts (sulphate or phosphate) as the only source of nitrogen and sodium

acetate or butyric acid as the carbon source. Certain amino acids could be utilized while nitrates could not. Sugars were of no nutritive value.

Lwoff and his co-workers verified this work and extended the method to other forms, emphasizing the importance of using sterile media (containing no other species of living organisms) and of knowing the chemical constitution of the media.

Numerous investigations have been made in recent years on various species of the Euglenida and of the Phytomonadida. In the light of present evidence *Euglena gracilis*, *E. klebsii* and *E. stellata* may be recognized as photoautotrophs. *E. deses* and *E. pisciformis* appear to be incapable of growth in inorganic media. *E. deses* has been grown on amino acids, whereas *E. pisciformis* apparently requires peptones. In darkness, *E. gracilis* can be grown in peptone media and is no longer dependent on photosynthesis. In a similar fashion *E. mesnili* has been grown in darkness and a strain entirely lacking chlorophyll has been maintained in the laboratory by Lwoff and Dusi (1938). On the other hand, there is no evidence that *E. anabena*, *E. deses*, *E. klebsii* and *E. pisciformis* are capable of continued growth in darkness. So in the genus *Euglena* all types of phototrophic nutrition must be recognized, and, in addition, a facultative heterotrophic type. There is a definite evolutionary trend here away from the primitive autotrophic condition.

All of the green Phytomonads investigated have photoautotrophic nutrition in the light and are capable of heteromesotrophic nutrition in darkness (e.g., *Chlamydomonas*, *Chlorogonium*, and *Haematococcus*). In the colorless Phytomonads we find a series beginning with *Polytoma uvella*, already discussed, and including *Polytomella caeca* which requires amino acids, and *Hyalogonium klebsii* which requires peptones. In this group, also, there is a definite trend toward the more animal-like methods of nutrition.

Much, then, has been accomplished in analyzing the nutrition of protozoans which normally take in their nutritive requirements in the form of dissolved substances. But what is definitely known about the nutrition of particulate feeders or holozoic forms?

Many attempts have been made to get at this problem by culturing holozoic protozoans in sterile non-particulate media of known composition. Lwoff (1932), in his treatise on the nutrition of protozoans, states that up until that time the only holozoic form which had been cultured successfully in a purely liquid medium was the ciliate, *Glaucoma piriformis*, originally isolated in pure culture by Lwoff in 1923.

Peters (1921) reported that he had cultured successfully the ciliate *Colpidium colpoda* in bacteria-free cultures on an ammonium-glycero-phosphate medium. Other workers tried to repeat his work without success, and in 1929 Peters reported that slow growing bacteria had been found in his cultures.

Lwoff found that nitrogen in the form of nitrates, ammonium salts, isolated amino acids, mixed amino acids, hydrolized silk and ereptone would not maintain continued growth of *Glaucoma piriformis* in bacteria-free cultures. However, peptones of muscle and peanut, produced either by pancreatic or peptic digestion, and yeast autolysate, supported luxuriant growth over many transfers. Lwoff found that this ciliate produces a proteolytic enzyme which hydrolizes a part of the peptones in the medium to amino acids. But as he found that natural mixtures of amino acids (e.g., ereptone) would not maintain continued growth,

he concluded that *Glaucoma* requires its nitrogen in a form no less complex than peptids, and that it actually absorbs peptones.

How does this ciliate, which normally obtains its nutrients by forming food vacuoles at the base of the cytopharynx, obtain them in a purely liquid medium? It is Lwoff's opinion that most of the peptids and peptones utilized enter directly through the pellicle. He found on the average from 1 to 5 liquid vacuoles in the *Glaucoma* examined and states that because of the rapid division of these ciliates it would not seem probable that all of the nutrients entered in the vacuoles formed. He states that it is not difficult to assume that these substances in the medium pass through the external membrane directly into the cytoplasm, when it is surely true that, as normal products of digestion in the vacuoles, they pass through the walls of the vacuoles into the cytoplasm. That such an assumption is reasonable is borne out by the fact that polypeptids are absorbed from the medium by *Polytoma*, *Chlamydomonas*, *Hematococcus*, and several Trypanosomes.

Lwoff attempted to cultivate several other ciliates and some amoebae in peptone media, but without success. He concluded in his 1932 monograph that these forms which would not grow in the peptone media were obligatory particulate-feeders. However, the normally holozoic forms in the following list have been successfully grown in bacteria-free cultures, according to the various authors listed (Table 1).

There seems to be little doubt about the validity of the results in the first seven cases. Loefer's strain of *Paramecium bursaria* is undoubtedly sterile, but this case differs from the others in that it has associated with it symbiotic green algae, and he has not been able to grow this species of *Paramecium* in pure culture when freed of the algae. In 1930 Glaser and Coria reported the pure culture of *Trichoda* and *Chilodon cucullus* in sterile buillon medium, but in 1935 they reported that these cultures did not thrive after numerous transfers. Thus they did not meet the critical test for pure cultures. No one, as yet, has verified the work of Reich on the amoeba, *Mayorella*.

The nitrogen requirements of all of these forms seem to be quite similar. In no case has it been possible to grow one of these forms on a single amino acid or on mixtures of amino acids. However, Elliott (1935) and Hall and Elliott (1935), working with two species of *Colpidium*, found that the best growth was obtained in those

TABLE 1

*Holozoic protozoans grown in pure culture*

| ORGANISM | AUTHOR | MEDIUM |
|---|---|---|
| 1. *Glaucoma piriformis* | Lwoff (1923) | peptone |
| 2. *Glaucoma scintillans* | Hetherington (1923) | peptone-glucose and yeast autolysate |
| 3. *Glaucoma ficaria* | Johnson (1935) | tryptone |
| 4. *Colpidium campylum* | Butterfield (1929) | peptone and yeast autolysate |
| *Colpidium campylum* | Hetherington (1933) | peptone-glucose and yeast autolysate |
| 5. *Colpidium striatum* | Elliott (1933) | tryptone |
| 6. *Loxocephalus granulosus* | Hetherington (1933) | peptone-glucose and yeast autolysate |
| 7. *Leucophrys patula* | Thomas (unpublished) | yeast autolysate |
| 8. *Paramecium bursaria* | Loefer (1934) | tryptone |
| *9. *Mayorella palestinensis* | Reich (1935) | peptone-glucose |

* This form is an amoeba—all the others are ciliates.

media high in amino acid content, indicating that these ciliates do utilize amino acids.

While the peptone media support good growth of the various ciliates reported, some acceleration of growth has been reported upon the addition of carbohydrates to the media. Lwoff (1925) found that *Glaucoma piriformis* utilizes maltose, levulose, galactose, and dextrose. Elliott (1935) reported that the two species of *Colpidium* studied were able to ferment these four sugars and in addition starch. Following the lead of v. Brand (1935), who, by the use of direct quantitative analytical methods, was able to show a difference in the rate of utilization of dextrose between several different species of Trypanosomes, Loefer (1938) was able to determine quantitatively the amount of dextrose used by cultures of *Colpidium campylum* and *Glaucoma piriformis*. Reich states that good growth occurred in his amoeba cultures only when dextrose, levulose or lactose was supplied.

But little is known about the use of fatty acids by these forms. Bond (1933) obtained "heavy growth" of *Colpidium campylum* with sodium salts of acetic, pyruvic and tartaric acids. Elliott (1935) reported that butyric acid accelerates the growth of *Colpidium striatum* in a restricted pH range.

It is interesting to note that the first seven species listed (and on which most of the studies have been made) are members of the same family—Frontoniidae. Another interesting fact is that one of these, *Leucophrys patula*, is, at least in one stage of its life cycle, a carnivorous form. Lepsi (1926) first reported that this form passes from a small bacterial-feeder to a large carnivorous form, and recently Dr. Waldo Furgason (personal communication) has been able to verify this, and to establish the nature of the life cycle. The fact that one carnivorous form has been grown in pure culture should be stimulating to further work of this kind.

Not many observations have been made on the exact way the nutrients are taken in by the different forms. Hetherington (1933) states, in referring to his cultures of *Colpidium campylum*, that "They are fatter than their typical condition in nature, always showing numerous food-vacuoles which are clear. Presumably they ingest the medium." Lwoff concluded that *Glaucoma piroformis* absorbs its medium to a large extent. The fact that this species of *Glaucoma* is sometimes found as a parasite in certain invertebrates and lower vertebrates (Epstein, 1926; Lwoff, 1932) might indicate that it has a greater capacity for absorbing nutrients directly through its pellicle than some of the others.

Many attempts have been made to culture numerous ciliates in sterile particle-free media, with negative results. Actually the first attempts to control the food of holozoic ciliates were made, not by the pure culture method, but by trying to culture different ciliates on single known kinds of bacteria. Many investigations on numerous protozoans have been made along this line; and, in the beginning, the purpose of such work was not so much that of understanding the nutrition of the organisms but rather that of obtaining greater control of the environment in experimental work on the organisms. Maupas (1888) and Jennings (1908) both suggested the need for such control of the food of protozoans but no real progress was made until the work of Hargitt and Fray (1917). These workers sterilized paramecia by repeated washings and then introduced them into infusions containing a single known kind of bacterium and into mixtures of several kinds. They found that *Bacillus subtilis* supported fair growth

of *Paramecium* when used alone but concluded that a mixture of several kinds formed a more suitable diet. Phillips (1922) also working with *Paramecium*, and Luck, Sheets and Thomas (1931), working with *Euplotes taylori*, reached essentially the same conclusion.

Other workers, however, have been successful in culturing several ciliates on a single strain of bacteria. In this category belong the results of E. and M. Chatton (1923), who grew *Glaucoma scintillans* on both *B. coli* and *B. fluorescens;* Hetherington (1933) who grew *Colpidium* on twelve different species used singly; Barker and Taylor (1931), who obtained excellent growth of *Colpoda cucullus* on *Pseudomonas fluorescens;* Johnson (1933), who cultured *Oxytricha fallax*, also on *Ps. fluorescens*, and several others. In the last two investigations just referred to the workers suspended the bacteria in a non-nutritive salt solution which resulted in a better quantitative control of the food.

It is not possible here to refer to all of the work of this nature which has been done in the last few years. Practically all of the investigators have found that some species of bacteria are good, some only fair, and some are actually toxic, when used as the only source of food for different protozoans. However, when one goes through the literature on this subject he is impressed with the fact that the various workers have not obtained the same results when using the same species of bacteria and the same species of protozoa.

TABLE 2*

*Suitability of various bacteria as food for Paramecium according to different investigators*

| SUITABLE | UNSUITABLE |
|---|---|
| *Bacillus subtilis* | *Bacillus subtilis* |
| *Bacillus coli* | *Bacillus coli* |
| *Bacillus proteus* | *Bacillus proteus* |
| *Bacillus cereus* | *Bacillus cereus* |
| *Bacillus aquatilis* | *Bacillus enteritidis* |
| *Bacillus lactis aerogenes* | *Bacillus Ravenli* |
| *Bacillus pyocyaneus* | *Bacillus prodigiosus* |
| *Bacillus candicans* | *Bacillus dendriticus* |
| *Bacillus megatherium* | *Bacillus flavescens* |
| *Bacillus niger* | *Bacillus fluorescens* |
| *Achromobacter pinnatum* | *Azotobacter* |
| *Erythrobacillus prodigiosus* | *Staphylococcus aureus* |
| *Flavobacterium brunneum* | *Aerobacter aerogenes* |
| *Pseudomonas fluorescens* | *Serratia marcescens* |
| *Pseudomonas ovalis* | *Escherichia coli* |
| | *Pseudomonas fluorescens* |
| | *Micrococcus flavus* |
| | *Bacterium plicatum* |

* From Leslie, 1940b.

Leslie (1940a and b) has reviewed the work done in this connection on *Paramecium*. Table 2 shows that the same bacterium has been reported as both suitable and unsuitable as food for this ciliate in a number of instances.

This recent study of Leslie is the most extended study of its kind up to the present. Using over thirty different species of bacteria, carefully standardized as to age and amount used, he tested their suitability as food for *Paramecium multimicronucleata*. The tests in most of the cases

were conducted for 30 days. Table 3 shows the results.

The list of bacteria investigated is not extensive enough to permit any generalizations about the suitability of large groups of bacteria as food for *Paramecium*. The result obtained by other workers is shown here, namely, that different strains of the same species may produce different results, e.g., the two strains of *B. subtilis*. Of particular interest here is the finding that the same species may vary in its suitability as food depending on the age of the culture used. Thus, *Pseudomonas fluorescens* was absolutely unsuitable when taken from 1-day-old cultures but was one of the best sources of food when taken from 4- to 30-day-old cultures. This lead, if followed, might result in the finding that many species of bacteria previously designated as unsuitable food organisms, are, under certain conditions, suitable food organisms.

TABLE 3[1]

*Different bacteria as food for Paramecium*

| CAT NO. | BACTERIUM | TOTAL PROGENY | DAYS | AVER. NO. | DIV. RATE | SUITABILITY |
|---|---|---|---|---|---|---|
| D-2 | *Bacillus mycoides* | 832 | 27 | 30 | 0.5 | poor |
| D-10 | *Bacillus cereus* | 1303 | 29 | 44 | 1.1 | good |
| D-20 | *Bacillus megatherium* | 1967 | 29 | 67 | 1.6 | good |
| D-21 | *Bacillus mesentericus* | 894 | 27 | 33 | 0.6 | poor |
| D-28 | *Bacillus niger* | 1086 | 29 | 36 | 0.8 | poor |
| D-41 | *Bacillus terminalis* | 942 | 27 | 34 | 0.7 | poor |
| D-39 | *Bacillus subtilis* | 655 | 15 | 43 | 1.0 | good |
| D-40 | *Bacillus subtilis* | 322 | 14 | 23 | 0.1 | poor |
| K-11 | *Escherichia coli* | 1034 | 29 | 35 | 0.7 | poor |
| K-12 | *Escherichia coli* | 774 | 30 | 25 | 0.2 | poor |
| A-5 | *Aerobacter cloacae* | 1711 | 29 | 59 | 1.4 | good |
| A-6 | *Aerobacter aerogenes* | 1372 | 29 | 47 | 1.1 | good |
| Al-2 | *Erwinea cartovora* | 1508 | 29 | 51 | 1.2 | good |
| C-1 | *Alcaligines fecalis* | 1670 | 29 | 57 | 1.4 | good |
| T-6 | *Proteus vulgaris* | 1224 | 27 | 45 | 1.1 | good |
| Z-1 | *Serratia marcescens* | 1260 | 27 | 46 | 1.1 | good |
| AA-2 | *Spirilla serpens* | 1077 | 30 | 35 | 0.7 | poor |
| Ad-13 | *Staphylococcus albus* | 597 | 30 | 19 | 0.0 | poor |
| Al-1 | *Erwinea atroseptica* | 789 | 30 | 26 | 0.3 | poor |
| Am-1 | *Phytomonas savastanoi* | 569 | 30 | 18 | 0.0 | poor |
| AM-3 | *Phytomonas tumefaciens* | 1910 | 30 | 63 | 1.6 | good |
| AO-1 | *Cellulomonas biazotea* | 618 | 30 | 20 | 0.0 | poor |
| F-1 | *Actinobacillus lignieresi* | 645 | 30 | 21 | 0.0 | poor |
| G-17 | *Corynebacterium ovis* | 702 | 30 | 23 | 0.1 | poor |
| N-1 | *Micrococcus luteus* | 547 | 30 | 18 | 0.0 | poor |
| N-2 | *Micrococcus ureae* | 731 | 30 | 24 | 0.2 | poor |
| O-6 | *Mycobacterium phlei* | 779 | 30 | 25 | 0.2 | poor |
| O-15 | *Mycobacterium smegmatis* | 803 | 30 | 26 | 0.3 | poor |
| O-21 | *Mycobacterium berolinensis* | 752 | 30 | 25 | 0.2 | poor |
| U | *Pseudomonas ovalis* | 2117 | 30 | 70 | 1.7 | good |
| *U-6 (5 lines) | *Pseudomonas fluorescens* | 1043 | 43 | 24 | 0.2 | poor |
| $U-6 (5 lines) | *Pseudomonas fluorescens* | 2462 | 41 | 60 | 1.5 | good |

[1] From Leslie, 1940b.

* 24-hour old bacterium.

$ 4-day old bacterium.

Investigations like those referred to above, while they do not give a real understanding of the nutrition of the protozoans involved in a chemical sense, are important because they have led to a much better control of the food factor in experimental protozoan work than was heretofore practiced.

A few workers have reported successful growth of ciliates in media containing dead microorganisms. Oehler (1919) reported growth of *Colpoda steinii* on dead bacteria and yeast; E. and M. Chatton (1923) cultured *Glaucoma scintillans* on dead bacteria; and Johnson (1936) was able to grow *Glaucoma ficaria* on dead bacteria, dead yeast and dead flagellates. Numerous other workers have not been successful. Luck, Sheets and Thomas (1931) used bacteria killed by a variety of chemical and physical means but could not obtain growth of *Euplotes taylori*. Phelps (1934), using similar methods, failed in attempts to culture *Paramecium aurelia*. Hetherington (1934) found that heat-killed bacteria would not support growth of *Colpidium colpoda*.

In the work on the use of dead bacteria an interesting situation is found. In certain instances the use of dead bacteria of a given species is unsatisfactory as food for a protozoan while the same bacterium in the living state is quite satisfactory as a source of food. E. and M. Chatton found that growth of *Glaucoma* would occur only after the culture media had previously been acted upon by the bacteria used. In other words, if the bacteria were removed from their medium and transferred with the *Glaucoma* to a new medium, no growth of the ciliates took place. This would seem to indicate that the dissolved products of the activity of the bacteria have an important effect on the growth of this form. Glaser and Coria (1935) obtained sterile cultures of two species of *Paramecium* in media containing either dead yeast or dead bacteria, and, in addition, liver extract and pieces of sterile rabbit kidney. Without the liver extract and the kidney their paramecia would not grow. Leslie (1939) tried dead bacteria as a source of food for *Paramecium* without success. However, in his work he obtained as good growth using bacteria from 30-day-old cultures as he did from 4-day-old cultures. In the 30-day-old cultures, 95 per cent of the bacteria were dead. When he used suspensions of bacteria from young cultures containing one-twentieth the original amount, reproduction was reduced by two-thirds. This would seem to indicate that the presence of a small amount of living bacteria permits the utilization of dead bacteria as food. On the basis of this Leslie has postulated that living *Pseudofluorescens* possesses "some growth-promoting substance or food factor for *Paramecium*, the lack of which in suspensions of dead *Ps. fluorescens* may account for its unsuitability."

What, then, is known about growth factors in the nutrition of Protozoa?

Lwoff (1938) has defined a growth factor for a given organism as a substance which that organism is incapable of synthesizing and in the absence of which the organism cannot multiply. Excluded from consideration are the elements, the energy-producing carbon-containing foods, and growth stimulants which the organism can produce itself.

M. Lwoff (1931) has shown that certain blood parasites, Trypanosomes, may be grown in peptone media if hematine is supplied. The hematine is a growth factor. It has been shown that the ciliate *Glaucoma piriformis* and three species of Trypanosomes require Vitamin $B_1$ for growth (A. and M. Lwoff, 1937, and M. Lwoff, 1937). Elliott (1939) demonstrated that the intact molecule of Vitamin

$B_1$ is required for growth of the ciliate *Colpidium striatum*. Vitamin $B_1$ is present in adequate amounts in the peptone medium. He destroyed the Vitamin B complex from the basic medium by adjusting the pH to 9.6 and then heating in the autoclave for 1 hour at 20 pounds pressure. Such treated medium would not support growth past the first transfer; but this treated medium, when crystalline thiamin chloride was added to it, supported excellent growth. Elliott further found that crystalline riboflavin and Vitamin $B_6$ (concentrate) could not supplant thiamin in the nutrition of *Colpidium*.

Hall and some of his students have shown that none of the ciliates which they have grown in pure culture will maintain growth in a gelatin-dextrose medium, where the only source of nitrogen is the gelatin. However, in 1938 Hall reported that when he added pimelic acid to this medium he was able to carry *Colpidium campylum* through six transfers with good growth. He says, "It thus appears that the failure of the ciliates to grow in gelatin is not dependent necessarily upon the amino-acid deficiencies of the gelatin. The implication is either that the missing amino acids are not essential to life of the ciliates or else that synthesis is possible in the presence of pimelic acid." This acid has been reported as a growth factor for the diphtheria bacillus by Mueller (1937). Cailleau (1938a and b) has found that the two flagellates, *Trichomonas foetus* and *Eutrichomastix colubrorum*, will not grow in the absence of ascorbic acid. Cailleau also found that cholesterol is indispensable for these same two flagellates and for one other, *Trichomonas columboe*. She states that when an alcoholic solution of cholesterol is added to the peptone medium it is precipitated in very fine particles and that the flagellates ingest and utilize these particles.

Lwoff (1932) in discussing the evolution of microorganisms points out that along with the morphological evolution there has been a physiological evolution involving a successive loss of functions as regards their abilities to utilize different compounds as nutrients. The following table (Table 4) illustrates this point.

Thus it is seen that the simplest forms can synthesize their proteins with nitrates as the only source of nitrogen, the next group requires ammonium salts, the next amino acids, the next peptones and finally the parasitic forms are dependent upon some special substance in addition to the peptones.

TABLE 4*

*Loss of functions in evolution of microorganisms*

| | NITRATES | AMMONIUM SALTS | AMINO ACIDS | PEPTONES | PEPTONES AND ACTIVE SUBSTANCE |
|---|---|---|---|---|---|
| *Aspergillus* | + | + | + | + | + |
| Yeasts, *Polytoma* | o | + | + | + | + |
| *Chlamydomonas* and *Haematococcus* (in the dark) | o | o | + | + | + |
| *Glaucoma pi iformis* | o | o | o | + | + |
| Parasitic bacteria and flagellates | o | o | o | o | + |

\+ organism can utilize.
o organism cannot utilize.
* From Lwoff, 1932.

Lwoff (1938) points out that this same idea—a loss of functions—applies with reference to growth factors. This has been shown for bacteria and it is indicated for protozoans in the next table (Table 5), with reference to Vitamin $B_1$.

Generally speaking, the first forms in the above table are able to synthesize both parts of the Vitamin $B_1$ molecule, the next group cannot synthesize the parts but can fuse them if they are furnished and finally *Glaucoma* and the Trypanosomes must be

furnished with the intact molecule of the vitamin. In discussing this, Lwoff points out that a veritable state of symbiosis exists in nature between many organisms—one organism producing one part of a necessary substance, another producing the other part of this substance.

In an earlier paragraph reference was made to the differences in results which have been obtained by various workers in their attempts to grow ciliates in sterile

TABLE 5*

*Ability to synthesize vitamin $B_1$*

| ORGANISMS | PYRIMIDINE | | THIAZOL | | VITAMIN $B_1$ | |
|---|---|---|---|---|---|---|
| | Need | Synthesis | Need | Synthesis | Need | Synthesis |
| *Polytoma obtusum* | o | + | o | + | o | + |
| *Polytoma uvella* | o | + | o | + | o | + |
| *Polytoma ocellatum* | o | + | + | o | o | + |
| *Polytoma caeca* | + | o | + | o | o | + |
| *Chilomonas paramecium* | + | o | + | o | o | + |
| *Acanthamoeba castellanii* | + | o | ? | ? | o | + |
| *Glaucoma piriformis* | o | o | o | o | + | o |
| *Strigomonas oncopelti* | o | o | o | o | + | o |
| *Strigomonas culicidarum* | o | o | o | o | + | o |
| *Strigomonas fasciculata* | o | o | o | o | + | o |

* From Lwoff, 1938.

culture on dead bacteria. A few have claimed success; several others have failed. In some quarters doubts have been raised as to whether those workers who claimed success with dead bacteria actually had sterile cultures, free from all living bacteria. Is it not possible, on the basis of the above-mentioned facts, to assume that some ciliates have the ability to synthesize all their needs from dead bacteria, while others may require something furnished by living bacteria? It seems reasonable to suggest that this attitude should be taken in future work. Certainly the field of growth factors in protozoans has only been scratched.

It seems worth while, at this point, to go back to Lwoff's original statements about the nature of the nutrition of *Glaucoma* in peptone media. He concluded that this ciliate absorbs substances as complex as peptids and even peptones directly from the medium and that the substances taken into the protoplasm through the surface must be comparable to the substances which enter the protoplasm from the food vacuoles as end-products of digestion when it feeds on particulate food. On this basis, isn't it a reasonable working hypothesis to assume that still other ciliates than those mentioned here may be successfully cultured on media of known compositions? That is, does it not seem plausible that substances comparable to end-products of digestion which can be utilized by other forms may be found, which, along with whatever growth substances may be necessary in each case, in a liquid medium may support growth of other normally holozoic forms?

Frisch (1937) has suggested that the pellicle of *Paramecium* is impermeable to water and salts and probably to gases. If this is true for *Paramecium* and other forms, and if the pellicle forms a barrier to the entrance of dissolved food materials, it still seems that the problem of their nutrition might be attacked by obtaining a properly constituted liquid medium to which is added a finely divided inert substance to facilitate the formation of vacuoles. That ciliates form vacuoles in suspensions of various materials is a common experience. It seems, then, too early in the studies of protozoan nutrition to conclude that a real understanding of the nutritive requirements of the large number of holozoic forms not successfully cultured on media of known composition up to the present will not be obtained.

Growth factors, by definition, are substances which an organism cannot synthesize. Substances formed by an organism which accelerate or stimulate growth are in another category. Although not forming a part of the basic nutrient requirements of an organism, such substances are related to the problems of nutrition and growth. As the production of growth stimulating substances has been described in a few species of protozoans in recent years, this matter is considered here briefly.

In 1921 T. B. Robertson reported that when he introduced two Infusoria (either *Enchelys farcimen* or *Colpoda cucullus*) into a small amount of fresh culture medium, the early rate of reproduction was more than double that of a single individual of the same species in the same volume of culture medium. Robertson designated this increased rate of reproduction as the "allelocatalytic effect." He postulated that a substance elaborated in the nucleus and given off into the medium at the time of cell division was the cause of this effect.

Numerous investigators, working with a variety of organisms, have tried to repeat Robertson's results, but without success. Johnson (1933), following leads from Chejfec (1929), who cultured *Paramecium* on different concentrations of *B. coli*, and Barker and Taylor (1931) who had observed the effects of different concentrations of *Ps. fluorescens* on the growth of *Colpoda*, was able to obtain results resembling those of Robertson by growing *Oxytricha fallax* in supra-optimal densities of *Ps. fluorescens*. These results were confirmed by Gause (1934), who worked with *Paramecium*. Such results, due to the effects of bacterial crowding, do not fit in with Robertson's postulate of the production of a growth stimulant. Phelps (1935), in studies on *Glaucoma* in pure culture, reported that he was unable to obtain any indication of the Robertson effect.

The status of this question remained unchanged until recently. Reich (1938) reported results from work on the amoeba, *Mayorella*, grown in bacteria-free cultures on peptone medium, which suggest the production of a growth stimulant by that form. Mast and Pace (1938) state that the colorless flagellate, *Chilomonas*, grown in an ammonium-acetate medium, produces a growth stimulant which soon accumulates in a culture and becomes a growth inhibitor. According to these workers their cultures were sterile. They have demonstrated that this substance is heat-labile. Quite recently (Mast and Pace, 1939) they have reported that this growth stimulating substance will pass through a cellophane membrane with a pore diameter of approximately 6 mu; and, they suggest that the diameter of the molecules of this substance is slightly less than 6 mu.

Kidder (1939), in a brief note, reports some results with cultures of *Colpidium campylum* grown in bacteria-free peptone-dextrose medium, in the explanation of which he postulates the formation of two substances, one a growth inhibitor which will pass through an asbestor filter and the other a growth accelerator which is absorbed on the filter.

The question of the production of growth stimulants by protozoans is still with us. Additional work is necessary before anything further can be said on the subject.

If this brief review is in a general way a fair statement of the status of our knowledge of protozoan nutrition at the present time, it is obvious that workers in this field still have many interesting and worthwhile problems to solve in future work.

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# NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that* THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Maud de Witt Pearl, Assistant Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *401 Hawthorn Road, Baltimore, Maryland, U. S. A.*

## BRIEF NOTICES

### EVOLUTION

GEOLOGY OF THE CLEVELAND REGION. *Pocket Natural History No. 9. Geological Series No. 1.*

*By Arthur B. Williams. Cleveland Museum of Natural History, Cleveland, Ohio.* 50 cents. $6\frac{3}{4}$ x $4\frac{3}{4}$; 61; 1940 (paper).

Although this little handbook was prepared especially for use in the Cleveland region, it also contains brief and interesting discussions on topics of general interest, such as geologic time, ancient American inland seas, culture as related to geology, and the influence of glaciation upon present distribution of human populations.

Within the state of Ohio there are two distinct physiographic areas: (1) the southeastern, unglaciated plateau of a rugged contour; and (2) the northeastern and western section of glaciated, smooth plateau land. The boundary between these two regions is roughly marked by the Portage Escarpment, a bold and steep rise from the glaciated area to the unglaciated section which corresponds generally with the southernmost extent of the glaciers of the great ice age of 20,000 years ago. Appended to the text are a short glossary and a list of bibliographic references.

### GENETICS

FARM ANIMALS: *Their Breeding, Growth, and Inheritance.*

*By John Hammond. Longmans, Green and Company, New York; Edward Arnold and Company, London.* $4.50. $8\frac{1}{2}$ x $5\frac{3}{8}$; viii + 199; 1940.

The ever increasing importance of agricultural products in our present world economy has been responsible for the effort, on the part of specialists in plant and animal husbandry, for continual improvement in their various fields. The successes, failures, and most promising lines for future work in the breeding and rearing of farm animals are neatly pointed out in this volume.

Part I of the text deals specifically with the physiology of sex, reproduction and growth of the five standard farm animals: i.e. horses, cattle, sheep, pigs, and poultry. The discussion of the sex of these animals as related to nutrition, endocrine activity, and general body health, constitutes an introduction to the more detailed accounts of the breeding season, the oestrus cycle, fecundity and fertility, viability of sperm and ova, sterility, artificial insemination, pregnancy, gestation, and parturition in the several forms. The problem of growth and development has been presented from the point of view of differential gradients in relation to nutrition and to the type of body build desired; the importance of this knowledge to both the farmer and the butcher is emphasized.

Part II discusses the relationship between genetics and modern methods and practice in animal breeding. Though a superior genetic make-up is admittedly

essential for the production of superior animals, the importance of selection and nutrition is not minimized.

The text is well illustrated, documented and indexed. It is an authoritative work that will find favor not only with the animal breeder, but with the general farmer whose breeding of animals is necessarily limited.

ELEMENTS OF GENETICS. *Mendel's Laws of Heredity with Special Application to Man. By Edward C. Colin. The Blakiston Company, Philadelphia.* $3.00. 8⅜ x 5⅝; xii + 386; 1941.

It has been the aim of the author to make this book interesting by weaving material on human genetics throughout the pages of an elementary text. In large measure the attempt has been successful. The simplest and accepted mechanisms of human heredity are presented in the early chapters, while those which are less well established are left to a separate section dealing largely with the inheritance of diseases.

In its scope the volume covers the same material as other elementary texts, but it contains little information on the statistical methods of measuring variations, which is an important factor, especially in the study of human inheritance. In placing his emphasis on man, Colin has neglected to show the widespread application of genetics to domesticated animals and plants. Although sparsely illustrated the book contains a glossary and a thorough index.

## GENERAL BIOLOGY

PHYTOPLANKTON AND PLANKTONIC PROTOZOA OF THE OFFSHORE WATERS, GULF OF MAINE. *Transactions of the American Philosophical Society Held at Philadelphia for Promoting Useful Knowledge. New Series, Volume XXXI, Part III. By Henry B. Bigelow, Lois C. Lillick and Mary Sears. American Philosophical Society, Philadelphia.* $1.75. 12 x 9¼; 91; 1940 (paper).

Collections of plankton made from the "Atlantis" at representative localities in the Gulf of Maine at various times of the year in 1933 and 1934 and in August, 1936, furnished the material for the two parts of this report. In the first—Numerical Distribution, by the three authors mentioned in the heading—planktonic protozoa were demonstrated to be at their numerical minimum from mid-autumn through the winter, with the regional variation wider in January than in any other month, with the most abundant winter population (900,000–1,000,000 per column) in shoal water close to Cape Cod and on the eastern part of George's Bank. Midsummer was marked as the season for maximum number of protozoa (about 4,000,000 per column).

> The next to the smallest count for protozoa (11,000 per column) was only about 1/8 as great as the smallest for phytoplankton; the largest for protozoa (10,700,000) about 1/1295 as great as the largest for phytoplankton; the grand average for protozoa only about 1/337 that for phytoplankton. These contrasts sufficiently emphasize the paucity of the waters of the Gulf of Maine in unicellular animals as contrasted with unicellular plants.

The results of the second part—Qualitative Composition of the Planktonic Flora, by Lois C. Lillick—show that:

> The scanty winter flora of the Gulf of Maine (usually dominated by Coscinodiscus, by Ceratium, or by other small peridinians) is succeeded by the vernal outbursts of diatoms and a decrease in the abundance of peridinians. This flowering results chiefly from the rapid multiplication of Thalassiosira. . . . The area of the Thalassiosira flowering expands northward along shore on both sides of the gulf, also southward and offshore into the eastern basin and to a certain extent into the western basin and over the eastern part of George's Bank. Active multiplication is briefest (2–4 weeks) in the eastern and southeastern parts of the gulf generally, longest in the northern coastal belt. After reaching its peak, Thalassiosira falls within a few days to an insignificant rank in the flora.
>
> Accompanying the eclipse of Thalassiosira, there is a flowering of Chaetoceros, which lasts from 4–6 weeks over the gulf generally (i.e., until late April–May). Once its peak of abundance is passed, Chaetoceros declines as abruptly in abundance as Thalassiosira.

Both papers are illustrated with maps,

the second also with diagrams, and each paper hasits own bibliography.

WILDLIFE CONSERVATION.
*By Ira N. Gabrielson. The Macmillan Company, New York.* $3.50. 9¼ x 6; xv + 250; 1941.

In this book the Director of the Division of Fish and Wildlife has written an authoritative treatise on the problems of conservation and the best means of meeting them. Conservation has been beset with continued bickerings and prejudices; the hunters and trappers, the nature lovers, the timber interests, the farmers, are but some of the many who have raised objections to whatever policy was pursued. Selfish motives, and more especially, a lack of appreciation and comprehension of what conservation consists of and what it aims to do, are in part responsible for a lack of mutual understanding. This book furnishes a broad foundation for a proper evaluation of conservation, stressing particularly the interrelations of soil, water, forest, and wildlife to the problem as a whole. The more detailed and analytical phases of conservation as exemplified by recent studies have been omitted—a wise procedure in view of the fact that this science is complex enough without introducing technicalities that would obscure the basic background that the author desires to establish.

The book fills an obvious gap. It is recommended that all those interested in our natural resources read it, especially those who have set ideas on the subject without really knowing why. Many photographs from the departmental files are used as illustrations. Unfortunately there is no bibliography.

PAPERS FROM TORTUGAS LABORATORY. *Volume XXXII. Carnegie Institution of Washington Publication No. 517.*
*Carnegie Institution of Washington, D. C.* $4.50 (cloth); $4.00 (paper). 10 x 6½; iv + 412 + 12 plates; 1940.

The papers from the Tortugas Laboratory have long been noted as significant contributions in the general field of marine biology. The present volume contains sixteen papers (by nineteen investigators) which deal with a variety of subjects, such as larval metamorphosis of the ascidian; the structure, composition, and growth of *Valonia*, and its reaction to light; the photosentivity of *Crangon* and *Panulirus*; the chromatophore system and chromatophore reaction of *Crangon* and *Pomacentrus*; the structure of zooxanthellae and their symbionic relation to *Tridachia*; and the ecology and geology of the Florida mangroves.

Of particular interest and significance is the long and detailed paper by Longley (late executive officer of the Tortugas Laboratory) and Hildebrand, in which the junior author, with the aid of Longley's notes and unpublished data, describes two new genera and fifteen new species of fishes common to the Tortugas. In a paper by Bullington, one new genus and nine new species of marine ciliates are described.

Each paper in the volume is provided with a short table of contents and a bibliography.

CARNEGIE INSTITUTION OF WASHINGTON YEAR BOOK *No. 39, July 1, 1939–June 30, 1940. With Administrative Reports through December 13, 1940.*
*Carnegie Institution of Washington, D. C.* $1.50 (cloth); $1.00 (paper). 10 x 6¾; xxxi + 326; 1940.

In the present issue of the Carnegie Year Book, fully half of the volume (171 pages) is devoted to biological and allied subjects. It is of interest to have at hand this summary dealing with the progress of the work throughout the year and the future lines of research in the different departments. The various monographs are seen by many as they are issued but no adequate conception of the detailed program of study can be obtained except through the Year Book. Following the reports of the Division of Plant Biology, the Department of Embryology, the Department of

Genetics, the Nutrition Laboratory and the Division of Historical Research there are reports on Special Projects in these various fields. The volume concludes with a list of publications issued by the Carnegie Institution during 1939–40 and a detailed index.

BIOLOGY

*By Howard M. Parshley. John Wiley and Sons, New York; Chapman and Hall, London.* $2.25. $8\frac{1}{2}$ x $5\frac{1}{4}$; ix + 232; 1940.

This book is a brief survey of the main facts and principles of modern biology. Its aim is to present the knowledge in this field which seems essential to a liberal education and therefore appropriate as the biological portion of a course in general science. A large subject has been brought within narrow limits by an elimination of technical detail which, while rather drastic, is intended to be not inconsistent with scientific accuracy and clarity. The excellent illustrations have been selected with special care. There is a bibliography at the end of each chapter, and, in addition, a complete list of references has been included in the appendix, which contains, in addition, a list of highlights of biological history and a glossary. A complete index concludes the volume. Designed as it is for a college survey course in science, this volume should effectively serve its purpose.

NATURE SMILES IN VERSE. *A Collection of Bi-illogical Poems.*

*Compiled by Bernal R. Weimer. Illustrations by Bobby Murray. B. R. Weimer, Bethany College, Bethany, W. Va.* $1.50. 9 x 6; x + 99; 1940.

This is an anthology of poems dealing with biological subjects, some of which are quite clever and all of which honestly try to be. Among the former are such old time favorites as Bert Leston Taylor's *The Dinosaur* and Charlotte Perkins Gilman's *Eohippus*, and among the latter numerous effusions that quite obviously were not intended for publication. The critical reader is likely to miss that delightful verse by Laura E. Richards about the "sculpin that was gulpin' of his tea, deary me," and to wonder why the compiler saw fit to commit mayhem on the masterpiece by Gelett Burgess about the lightning bug and the measuring worm.

## HUMAN BIOLOGY

FIRST EXPEDITION OF VARGAS INTO NEW MEXICO, 1692.

*Translated, with Introduction and Notes by J. Manuel Espinosa. The University of New Mexico Press, Albuquerque.* $4.00. $10\frac{1}{2}$ x $6\frac{3}{4}$; xi + 319; 1940.

The Spaniards, in enlarging their possessions in the Western World after their conquest of Mexico, pushed far north into what is now New Mexico and Arizona. It had been their expectation that this region, a land of mystery, would be as productive of wealth as were the countries to the south. Coronado, however, returned empty-handed so far as gold and silver were concerned, but he brought marvelous tales of what lay beyond the regions he had traversed. During the seventeenth century the non-aboriginal population of New Mexico never exceeded 3,000. Santa Fe had been established as the capital of the province in 1610. The pueblo Indians, of a peaceful nature, were taught the language of their conquerors and practiced outwardly their religion. The governors of New Mexico, being far from the main seat of authority, failed as the years passed by to carry out Spain's humane Indian laws. Growing discontent among the natives finally resulted, in 1680, in a successful revolt. For twelve years the Indians held New Mexico as their own, in spite of large sums of money spent by the Spaniards in reconquest. By this time it was realized that the real value of New Mexico to the Spanish provinces lay in the fact that this region was a bulwark of defense not only against Indian attacks from the whole northern frontier but also from the French and Indians who were pushing in from the east.

Early in the last decade of the seventeenth century Diego de Vargas was given the task of reconquest. A preliminary expedition in 1692 paved the way for a much larger expedition in 1693, with settlers, missionaries, and live stock. Many pueblos were found willing to accept Spanish rule, while others, fearing punishment for the crimes of 1680, were subdued with difficulty. Victorious campaigns of Vargas in 1694 were followed by increased numbers of settlements and within the next few years New Mexico was laying the foundations of self-sufficiency and permanency. What scattered rebellions occurred Vargas met with a series of swift revengeful campaigns.

In the present volume following the Introduction, which we have so briefly summarized, the documents which deal with the first phase of the reconquest of New Mexico are given in full. These are as follows:

Document I. Report of the finance committee of the government of New Spain, Mexico city, May 28, 1692, officially authorizing Don Diego de Vargas to reconquer New Mexico (5 pp.); Document II. Vargas' campaign journal and correspondence, August 21 to October 16, 1692 (118 pp.); Document III. Vargas' campaign journal correspondence, October 16, 1692, to January 12, 1693 (112 pp.); Document IV. Letter from Don Diego de Vargas to the Conde de Galve, El Paso, January 12, 1693, concerning the settlement of New Mexico (12 pp.); Document V. Report of Conde de Galve to Don Diego de Vargas, Mexico city, November 24, 1692 (7 pp.); Document VI. Report of the general junta, Mexico city, February 25, 1693 (7 pp.); Document VII. Order of the Conde de Galve to Don Diego de Vargas, Mexico city, April 18, 1693 (5 pp.).

We have in this book not only new light on a stirring chapter in the history of the American frontier, but much interesting material on the pueblo Indians. The volume is carefully indexed.

THE MAYA AND THEIR NEIGHBORS. *Limited Edition.*

*By Clarence L. Hay, Ralph L. Linton, Samuel K. Lothrop, Harry L. Shapiro, George C. Vaillant et al. D. Appleton-Century Company, New York and London.* $6.00. $9\frac{3}{8}$ x 6; xxiii + 606; 1940.

It is difficult in a brief space to do justice to this scholarly book, written by a group of specialists each one of whom is a student of some particular phase of Middle American archaeology. Its purpose is to offer a summary of current opinion in this field which will be "a critical guidance toward an understanding of the basic nature of the subject or toward following the general direction of the research." A vast literature has accumulated concerning Middle American archaeology but it is too formidable a list for the consideration of the student in other lines of work or the serious lay reader who is in search of background reading on Indian civilization.

Within the covers of this book will be found a fine collection of essays, thirty-four in number, grouped under four section headings. In Part I, The Background of the Maya, an analysis of the basic factors underlying the racial affiliations of the American Indian is given, followed by discussions on such subjects as the basic physical factors affecting Middle America, food supplies essential for existence, native languages, and an analysis of the different linguistic maps made for the Middle Area. In Part II, The Maya, the essays deal with the development of Maya civilization in relation to the problems of Middle American culture in general, the latest research in the highest centers of Maya civilization, the history of the decipherment of the Maya inscriptions (a feat of scholarship almost on a par with the formulation of the original graphic system), Maya and Christian chronologies, astronomy, architecture, ceramics, skeletons from the Cenote of Sacrifice at Chichen Itzá and the transformation of the modern Maya from the manner of life of their ancient predecessors. In Part III, The Northern neighbors of the Maya, the discussions are on the basic difference between the Middle American cultures and those of North and South America, the contemporaneity of the advanced civilizations of the Toltec and Zapotec, archaeology and pottery, and Mexican influences upon the Indian cultures of the southwestern United States in the 16th and 17th centuries. Part IV. The Southern neighbors of the Maya, is concerned with the southern limits of Maya civilization, archaeological

remains of Honduras, non-Maya monumental sculpture of Central America, the diffusion of culture from Middle America and the effect on the cultures of South America, and South American penetrations in Middle America. The final essay is a critical synthesis of the essays contributed to the volume in their relationship to American anthropology as a whole.

Accompanying the text are 20 plates, 40 illustrations, a linguistic map of Mexico and Central America, and 11 tables. A bibliography of 103 pages and an index conclude the volume.

THE MAORI PEOPLE TODAY. *A General Survey.*

*Edited by I. L. G. Sutherland. Issued under the Auspices of The New Zealand Institute of International Affairs and The New Zealand Council for Educational Research. Oxford University Press, New York.* $4.00. $8\frac{1}{2}$ x $5\frac{1}{4}$; xiii + 449; 1940.

The New Zealand Institute of International Affairs, an unofficial and non-political body, has for its object the promotion of an understanding of international questions and problems particularly in so far as these may relate to New Zealand, the British Commonwealth, and the countries of the Pacific Area.

The nine authors, who contribute the twelve chapters of the present volume, are all specialists on some phase of Maori life, and one of them, Sir Apirana Nyata, is an outstanding member of the Maori group. They present a study "designed to put on record the present position of the race and to discuss its problems at what appears to be a critical stage in its history."

The Maori people, one of the most interesting of the Polynesian races, made their great migration from the tropical islands of the Eastern Pacific to New Zealand about six centuries ago (*circa* 1350). Although new modes of living, necessitated by a much colder climate, and variations in their tribal customs, due first to their long isolation from other Polynesians and later to their contacts with European settlers, created many changes in their customs, the background of their culture is still that of the Polynesians. We are given much that is of interest concerning the main features of the Maori and early European settlers, tribal organizations, economic conditions, education, arts and crafts, and religious influences, with a final summing up of the present Maori situation by Sutherland.

The volume contains a number of illustrations, a glossary, a brief list of references and a detailed index.

NORWEGIAN MIGRATION TO AMERICA. *The American Transition.*

*By Theodore C. Blegen. Norwegian-American Historical Association, Northfield, Minnesota.* $3.50. $8\frac{3}{4}$ x $5\frac{1}{2}$; xii + 655; 1940.

In an earlier monograph Blegen described the Norwegian immigration of the first half of the 19th century and the factors that determined it. In this volume the account is continued and concerns primarily the processes which led to the integration of the Norwegian group with the rest of the population of this country. The author depicts in detail the conditions of the immigrants when they arrived, the culture that they brought with them and their reactions to the culture of their adopted country. The immigration was in general by family groups and the immigrants on the whole appeared as closed colonies which centered around the church. Because of this, the individuality of the Norwegian settlements was retained for some time and until, through the public schools, the offspring of the immigrants gained access to the mores of this country. The most important political event which transformed passive participation in the affairs of the country to an active one was the Civil War. Then, the Norwegians began to identify themselves with the nation that had given them hospitality. In describing the folkways of the immigrants, the development of their schools and of higher education, and their transformation into Americans, the author has had recourse to original sources. Moreover, the style in which the subject is written is far from pedantic so that this work makes for enjoyable reading besides presenting a clear-cut picture

of the pattern of the processes of amalgamation of peoples within our country.

NEW HAVEN NEGROES. *A Social History. By Robert A. Warner. Yale University Press, New Haven; Oxford University Press, London.* $3.50. 9 x 5¾; xiv + 309; 1940.

It is to be hoped that some day the social relations between Negroes and whites will attain a status satisfactory to both groups. In the meantime thoughtful persons and especially those who sincerely believe in the principles of freedom, cannot help but be distressed by the white man's actions with respect to the Negro. The account presented in this book is not very different from that which can be reported from other communities, except that New Haven is one of the oldest civilized centers of the country so the conduct of its population seems even more unpleasant. In Connecticut the Negroes were emancipated in 1784 but still in 1864 they were little better off than the Negroes elsewhere and had not made appreciable progress toward the achievement of their rights. The author emphasizes two points about the history of the Negro in New Haven. The first is the struggle to be permitted to have formal education. The long fight and the political partisanship involved are tersely described and make for thrilling reading. The second point is the formation of castes. For the Negro today as well as for the whites the circulation of the social classes is being reduced considerably. As in all other communities, so in New Haven the Negro occupies the lowest rank, and for some reason the author believes that this is an indication of progress on the part of the Negro. Although rather narrow in outlook, this monograph is interesting because of its subject and the efforts of the author to make an extensive survey of the situation and its origins.

THE IMMIGRANT IN AMERICAN HISTORY. *By Marcus L. Hansen. Harvard University Press, Cambridge.* $2.50. 8 x 5¼; xi + 230; 1940.

This book consists of nine essays on a subject about which the author was one of the foremost specialists. Several of the broad aspects of the immigration to this country form the topics of these essays; first of all being the movement of the first half of the 19th century and all the hardships associated with leaving the country of origin and settling in the new country. The author has made use of contemporary accounts and they are both tragic and amusing. Preoccupations relative to religion were foremost in the minds of the immigrants. The process of adapting religious customs and views to a new environment was one factor responsible for the multiplicity of sects into which some of the denominations split. Hansen sought also to evaluate the contributions of the several national groups to the civilization of this country. He cast a doubtful eye on the pretensions of the descendants of the several foreign groups but was himself unable to arrive at any sound measure of their contributions. Without doubt some time will pass before an adequate and objective determination can be achieved. It cannot be said that new facts are brought out in this volume, but the presentation of the subject will certainly stimulate a clearer understanding of the elements that entered into the formation of our nation.

ON SAFARI.

*By Theodore J. Waldeck. With Illustrations by Kurt Wiese. The Viking Press, New York.* $2.50. 8½ x 5½; 208; 1940.

*On Safari* is an excellent collection of adventure stories as well as an elucidative text for embryonic explorers. The author, a famous explorer, has selected anecdotes from his many African adventures and the result is a collection of exciting tales of life on the Dark Continent. These stories are also instructive as to what Africa demands in courage, scientific knowledge, skill, and leadership to unravel her many secrets and survive all dangers on safari. Waldeck's first experience, about which he writes most

entertainingly, was at the age of 18 on the Duke of Mecklenburg's expedition in 1912. His second African trip occurred seven years later on an expedition under the leadership of Professor Leo Frobenius to the mysterious city of Makala in Zululand. Later, he organized his own expeditions, the first of those being the Waldeck-Smith Expedition in 1924. One of his most interesting African experiences occurred in Abyssinia with the Gallas, Coptic Christians, who almost killed him and his partner Smith, then cured them when they lay ill of fever, and later entertained the explorers in regal, if rather unhygienic and crude, fashion. Lastly, the author relates the exciting story of his initiation into the Secret Order of Lion Men of the Masai, one of the oldest fraternal organizations in the world. Kurt Wiese executed the excellent illustrations which accompany the text.

BIOLOGIE DER GROSSSTADT. *IV. Frankfurter Konferenz für medizinisch-naturwissenschaftliche Zusammenarbeit am 9. und 10. Mai 1940.*

*Edited by B. de Rudder and F. Linke. Mit Unterstützung der Stadt Frankfurt a. M. Theodor Steinkopff, Dresden and Leipzig.* RM. 8 (in Germany); RM. 6 (outside of Germany). $9\frac{1}{4}$ x $5\frac{3}{4}$; xi + 210; 1940 (paper).

The papers included here were read at the Fourth Frankfurt Conference for Medical and Scientific Cooperation, held on May 9 and 10, 1940. In the first paper "Anthropology of the City," von Verschuer discusses the probability of a relationship between urbanization and (a) increase in body growth and (b) acceleration in development of city children as compared with those in rural districts; fertility and the birth rate. His conclusion is that the large city is "the grave of racial strength and the cultural endowment of our people." One other paper, by Bennholdt-Thomsen, treats the developmental acceleration of the city child. Other papers are concerned with: the origin and growth of cities (W. Polligkeit); characteristics of industrial cities (W. Brepohl); animal populations of cities (H. Giersberg); influence of the urban milieu on diseases of children (B. de Rudder); the differences between country and town from the psychiatric viewpoint (K. Kolle); and various offerings on the health, nutrition, and hygiene of the city dweller.

Bibliographic references or notes and illustrations accompany some of the papers. Author and subject indices are provided for the volume.

DEALING WITH DELINQUENCY. *Yearbook National Probation Association 1940.*

*Edited by Marjorie Bell. The National Probation Association, 1790 Broadway, New York.* $1.75 (cloth); $1.25 (paper). $8\frac{3}{4}$ x $5\frac{3}{4}$; 341; 1941.

This volume contains the papers read at the 1940 meeting of the National Probation Association held at Grand Rapids, Michigan. Twenty-two articles are segregated under nine different headings. These include the more important aspects of the problems of treatment and prevention of crime and delinquency, creation of clubs and playgrounds to curb juvenile delinquency, social service work associated with probationary activities, administration of probationary and parole systems, popularization of law enforcement and crime prevention measures. In addition there is included in this issue a digest of current legislation concerning probation and parole systems and juvenile courts, and a statistical and financial statement of the Association's work during 1940. At its inception the National Probation Association resembled in certain respects the church organizations with their holy, if unapproachable, objectives. Such attitude was soon abandoned and as one can see from the present report, the members of the Association view the broader sociological and biological factors in crime and attempt to direct their activities accordingly. If this attitude continues and is further extended the great contributions made by the Association towards

crime prevention will be still more increased.

MAN: *The Mechanical Misfit.*

*By G. H. Estabrooks. The Macmillan Company, New York.* $2.50. 8 x 5¼; 251; 1941.

As the title indicates, the author of this volume endeavors to prove that man is a mechanical misfit and will sooner or later be as extinct as the dinosaur and the saber-toothed tiger. In support of this argument, it is claimed that the skeleton is deteriorating, the internal organs are inadequate, and, worst of all, the brain and nervous system is a curse to man. Similarly, man by thwarting nature's device of weeding out the unfit, has preserved the unfit and encouraged their reproduction, so that natural selection is becoming less and less effective. The author believes that industrial progress, inventive genius and preventive medicine are really "softeners of the race," rendering it unfit to survive in the raw world of nature if its artificial safeguards should ever be swept away. The solution for all of these problems, says the author, is to sterilize all the unfit for one generation, and thus solve all the hereditary problems at one blow, and at the same time eliminate war. Although many readers may not agree with the author's indictments and conclusions, they cannot help but find them immensely stimulating and provocative. The book is indexed, but has no bibliography.

FAMILY INCOME AND EXPENDITURES: *Middle Atlantic, North Central and New England Regions. Part 1, Family Income. U. S. Department of Agriculture Miscellaneous Publication No. 383. Consumer Purchases Study. Farm Series.*

*By Dorothy S. Martin, Day Monroe, Dorothy S. Brady, and Elizabeth Phelps. Government Printing Office, Washington, D. C.* 25 cents. 9⅛ x 5¾; iv + 258; 1940 (paper).

FAMILY INCOME AND EXPENDITURES: *Five Regions. Part 2, Family Expenditures. U. S. Department of Agriculture Miscellaneous Publication No. 396. Consumer Purchases Study. Urban and Village Series.*

*By Dorothy S. Brady, Day Monroe, Elizabeth Phelps, and Edith D. Rainboth. Government Printing Office, Washington, D. C.* 40 cents. 9⅛ x 5¾; iii + 410; 1940 (paper).

Earlier numbers of both the Farm Series and the Urban and Village Series have been noticed in these columns from time to time as they have appeared. The present parts follow the general pattern and purpose of the earlier numbers, namely to show how families in different sections of the United States, in different types of communities, and in different income and occupational groups spend their money.

ASSAM ADVENTURE.

*By F. Kingdon Ward. Jonathan Cape, London.* 12s. 6d. net. 7⅞ x 5¼; 304 + folding map; 1941.

Captain Ward, accompanied by Tashi and Pemba, two Sherpas from Darjeeling, made an expedition of 1,100 miles from Assam over the Great Himalayan Range into the rugged wilds of Southern Tibet. The story of this journey, made in 1935—much of it over territory previously unexplored—is interestingly told. Superimposed are observations of the flowers, people, and geography of the Balipari Frontier Tract made on a second visit three years later. The book should be of interest to several types of readers. The descriptions of the plant finds will fascinate botanists and gardeners, particularly those interested in rock gardens, for which many of the Tibetan plants are most suitable. There is sufficient adventure to attract the general reader interested in travel books. The observations of the people and their customs will interest the ethnologist, and the descriptions and maps of "new" territory, the geographer. Appendix I gives a summary of the marches and Appendix II a list of Tibetan

plants. There are sixteen photographs showing plants, people, and places.

ACCULTURATION IN SEVEN AMERICAN INDIAN TRIBES.

*Edited by Ralph Linton. D. Appleton-Century Company, New York and London.* $4.00. $8\frac{3}{4}$ x $5\frac{3}{4}$; xiii + 526; 1940.

Herein are presented tribal studies on the acculturation process in seven American Indian tribes, namely: the Puyallup of Washington, the White Knife Shoshoni of Nevada, the Southern Ute of Colorado, the Northern Arapaho of Wyoming, the Fox of Iowa, the Alkatcho Carrier of British Columbia, and the San Ildefonso of New Mexico. The seven reports, presented according to a detailed "Outline for report on acculturation in any given tribe" which appears in the introduction, represent original field work by the author. Many new unpublished ethnological data are given. Linton briefly summarizes each of these studies and in the last three chapters of the text defines acculturation and the culture concept and discusses the processes of culture change, culture transfer, and the distinctive aspects of acculturation. The volume is indexed.

CATTLE, HORSES AND MEN OF THE WESTERN RANGE.

*By John H. (Jack) Culley. Illustrations by Katherine Field. The Ward Ritchie Press, Los Angeles.* $3.00. 9 x 6; xvi + 337; 1940.

Here is a truly delightful account of one of the colorful periods of American history—from about 1865 to 1900—which had to do with the development of the range cattle business in the western half of the United States. The author has been one of the actors in the great drama of the west and speaks authentically of the characters and events comprising the life in this romantic period of our history. The first part of the book deals with life on the famous Old Bell Ranch, in New Mexico, of which the author became ranch manager; the second part with horses as Culley learned to know, understand and train them during his years in the ranch business. In the third part of the volume, the cattle and men who were the major participants in this saga of the west are described in detail. The delightful illustrations are by Katherine Field. The book makes entertaining and instructive reading and has been indexed for the use of scholars.

EVIDENCE OF EARLY INDIAN OCCUPANCY NEAR THE PEAKS OF OTTER, BEDFORD COUNTY, VIRGINIA. *Smithsonian Miscellaneous Collections, Volume 99, Number 15.*

*By David I. Bushnell, Jr. Smithsonian Institution, Washington, D. C.* 20 cents. $9\frac{1}{2}$ x $6\frac{1}{4}$; 14 + 5 plates; 1940 (paper).

In this brief monograph the author has outlined the evidence pointing to early Indian occupancy in the vicinity of the Peaks of Otter, Bedford County, Virginia. The Mons site, so called because part of the settlement was found on the grounds of the recently demolished resort hotel, Hotel Mons, was exposed during the spring of 1940 during work on the extension of the Skyline Drive. Following a discussion on the region in which the ancient Indian settlement was found, there is a descriptive section, with accompanying plates, on the artifacts, including two Folsom points and pottery fragments, uncovered on the site. There are nine illustrations—five plates and four figures, the latter including a reconnaissance map of Bedford.

SOCIAL AND ECONOMIC ASPECTS OF SWEDISH POPULATION MOVEMENTS 1750–1933.

*By Dorothy S. Thomas. Macmillan Company, New York.* $6.00. $8\frac{1}{4}$ x 5; xxiii + 487; 1941.

The Swedish vital and economic statistics are generally regarded as the most complete of any such statistics, and contain the longest continuous series of census data. Much use has been made of these data by several statisticians and the author has sought to bring the series

further to date and to complement the data with other pertinent information. For the years 1750 to 1933 the statistics given concern the population and its movements, agriculture and industry. For a shorter number of years, from 1895 to 1933, the data refer to urban and rural communities into which Sweden is segregated. With minor exceptions the author has limited herself to an exposition of the statistics in a manner not much more discursive than the yearbooks published by governmental agencies. However, credit is due Thomas for making such valuable data easily available to all students.

RASSENKUNDE UND RASSENGESCHICHTE DER MENSCHHEIT. *Erster Band. Die Forschung am Menschen. Fünfte Lieferung (Bogen 32–39). Zweite umgearbeitete und erweiterte Auflage.*

*By Egon Freiherr von Eickstedt. Ferdinand Enke Verlag, Stuttgart.* RM. 10. 10½ x 7; 497–624; 1940 (paper).

Numbers 1, 2, 3, 4, 6, and 7 of this second edition have already been noticed in these columns at various times since Volume 3, Number 3. As in these earlier *Lieferungen* the revision and additions in the present number have been extensive. Fully annotated, it treats type analyses and type characters, and begins the discussion on methods of research on the make-up of population groups (studies on twins, number of children in families, paternity tests, pedigrees, statistics on marriage, population, migration, etc.)

THE WARS OF THE IROQUOIS. *A Study of Intertribal Trade Relations.*

*By George T. Hunt. University of Wisconsin Press, Madison, Wisconsin.* $3.00. 9⅛ x 6; 209; 1940.

The subtitle is the key to the nature of this penetrating study. The author does not treat the Iroquois as aggressors who made war for its own sake. He considers them as a people who were primarily traders, and who, when faced with the possible loss of their trade, chose to fight to maintain it. In the end they became the dominant tribe in the so-called League of the Iroquois, influential far to the north and south of their territory, and accordingly valuable as allies of the English in the wars with the French in Canada. It is interesting to note that the author does not think the Indians were as well supplied with firearms as is commonly supposed.

VERHANDLUNGEN DER DEUTSCHEN GESELLSCHAFT FÜR RASSENFORSCHUNG. *Band X. Vorträge gehalten am 24. und 25. März 1939 auf der 10. Tagung in München. Sonderheft zum XVI. Jahrgang des Anthropologischen Anzeigers.*

*Edited by B. K. Schultz. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.* RM. 16.95. 10 x 6½; xx + 168 + 17 plates; 1940 (paper).

The list of authors of the 24 lectures contained in this volume includes Th. Mollison, J. Schwidetzky, H. Weinert and O. Reche, among others well known in their respective fields. The lectures deal with newer anthropological findings, race history and ethnology, and a few miscellaneous items such as sex differences in the performance of sports. Most of the papers are based on German material.

INDIAN POPULATION PROBLEMS. *Report and Proceedings of the 2nd All-India Population and 1st Family Hygiene Conference, 1938.*

*Edited by G. S. Ghurye. Karnatak Publishing House, Bombay.* Rs. 5. 9½ x 6⅝; 332 + xii + [7]; 1940 (paper).

The papers collected in this volume are organized according to the sections before which they were read: Birth control and sterilization; Medical problems and problems of sex; Maternity and child welfare; Housing and health; Vital statistics; Economics; Sociology; and Nutrition. Some abstracts of papers received but not read at the meetings are included at the ends of the proper sections. Most of the

material is based on studies made in India.

BORN THAT WAY.
*By Earl R. Carlson. The John Day Company, New York.* $1.75. $7\frac{3}{8}$ x 5; ix + 174; 1941.

This is an autobiography written to offer encouragement to the physically handicapped. Such a person who reaches the goal he has chosen merits praise from all of us. When that person then uses the knowledge he has gained in his own struggle for success to help others crippled as he is, we feel that his success is well deserved. Its very nature makes this a personal story, but it is not sentimental; rather, it is an account of a life-long campaign which requires a great deal of energy and will power.

## ZOÖLOGY

INSECT PESTS.
*By W. Clunie Harvey and Harry Hill. H. K. Lewis and Company, London.* 10s. 6d. net. $7\frac{1}{4}$ x $4\frac{1}{2}$; ix + 292; 1940.

INSECT PESTS OF FARM, GARDEN, AND ORCHARD. *Fourth Edition.*
*By Leonard M. Peairs. John Wiley and Sons, Inc., New York and London.* $4.00. 9 x $5\frac{3}{4}$; xvii + 549; 1941.

The first of these two volumes is concerned with insects that are a nuisance to human beings. The present conflict in Europe, with its evacuation problems and the herding together of military personnel and civilians has brought to the attention of public health, medical, and commercial authorities in England the importance of insect control. Part I of this handbook deals with the appearance, life history, characteristics and habits, control or eradication, etc., of the bed-bug, flea, louse, cockroach, cricket, silver-fish, ant, itch mite, book lice, earwig, wood lice, and housefly. Part II presents the techniques of fumigation with various gases, and other insect specifics, the disinfections of homes, foodstuffs and ships, with chapters on legislative control and human toxicology. The volume is illustrated and indexed.

Peairs, co-author with E. D. Sanderson of the previous edition of the second of these two books (cf. Q.R.B., Vol. 7, p. 362) has, at the request of Sanderson, assumed full responsibility for the present revision. The same general plan of presentation has been maintained but the material has been revised and rewritten to include the latest advances in the field of economic entomology. Account has been taken of the fact that changes in agricultural procedures, changes in the composition and use of insecticides, and changes in plant constitution and immunity, have drastically changed the economic importance of numerous insects; some harmful ones have become harmless or even helpful, while conversely, some quite harmless or even beneficial insects have become significant pests. The work is well documented throughout with bibliographic references, and is generously supplied with illustrations. A very useful index is appended.

ENTOMOPHAGOUS INSECTS. *First Edition.*
*By Curtis P. Clausen. McGraw-Hill Book Company, New York and London.* $7.00. 9 x $5\frac{3}{4}$; x + 688; 1940.

Into this volume the author has brought all of the important work—and this has reached formidable proportions—which has been done on entomophagous insects. It "represents as nearly as possible, what the author himself would like to have had available while engaged in field work upon insect parasitology and the biological control of insect pests." Insects are their own worst enemies. It is estimated that about 224 families, in 15 orders, have in some degree the entomophagous habit—a fortunate habit for the present human race, since the equilibrium in the insect population is held "at a sufficiently low level to permit the existence of plant and animal life as we know it today."

Clausen, with his wide understanding of the subject, dwells less on the predator than on the parasitic insects. Predators

are those forms that usually have a free-living larval existence and require a number of hosts to bring them to maturity. Their food is usually the same in all stages. The parasitic forms develop, in the larval stage, either internally or externally on a single host individual, the latter eventually dying as a result of this relationship. The adults, almost always free-living, depend upon a different kind of food than do the larvae. The immature stages of the parasitic insects exhibit a wide range in habit and in form, growing out of the adaptations imposed by the forms and habits of their different hosts.

Fully half of the volume is devoted to the Hymenoptera, among which are to be found the most important parasites useful to man, not only as regards the number of species having the entomophagous habit but in the effectiveness with which they attack the insect pests of agricultural crops. The Diptera and Coleoptera and less important groups follow. Detailed discussions are given of host preferences, biology and habits, development and life cycle, and immature stages. Numerous figures are included in the text and the list of references covers 46 pages. A carefully planned index concludes this important text.

THE INDO-CHINESE FOREST OX OR KOUPREY. *Memoirs of the Museum of Comparative Zoology at Harvard College, Volume LIV, Number 6.*

*By Harold J. Coolidge, Jr. Museum of Comparative Zoology, Cambridge, Massachusetts.* $3.50. 12 x 10; 115 + 11 plates; 1940 (paper).

This rare animal has only been known for about ten years. There is, or was at the time this monograph was written, a four-year-old male in the Vincennes Zoo to which Urbain has given the name *Bos* (*Bibos*) *souveli*. The present description is based on a fine specimen of an old adult bull, shot in Cambodia during the winter of 1938–39, and presented to the Museum of Comparative Anatomy at Harvard. Little is known at present about the distribution or frequency of the kouprey as no big-game hunting has been done over the forest areas north of Cambodia.

In comparing the kouprey with the only two living kinds of wild taurine cattle from the forests of southeastern Asia, the gaur and the bantin, Coolidge finds that the "principal significant external differences by which the kouprey differs from the two others are limited to the marking of the lower legs, the peculiar horns [fringed near the tips] with their relation to the skull and the elongated tail." Detailed descriptions are given of the differences and similarities between the hides and skeletons of the kouprey, gaur, and bantin, and comparisons are made with allied genera, both living and fossil forms. "The kouprey skull, while clearly that of an Asiatic taurine, shows more primitive features than any of the other surviving forms." It is possible that further research may reveal the kouprey to be the living representative of the probable ancestor of neolithic domesticated cattle.

Seventeen tables of measurements, 10 figures and 11 plates exhibit the main descriptive features of the text. A brief bibliography for the kouprey is given and there is also a lengthy general bibliography.

ZOOLOGICA. *Scientific Contributions of the New York Zoological Society, Volume XXV, Part 4, Numbers 25–34.*

*New York Zoological Society. Zoological Park, New York.* $2.35. 10½ x 5½; 202; 1940.

This number contains the following papers:

Eastern Pacific Expeditions of the New York Zoological Society. XXII. Mollusks from the West Coast of Mexico and Central America. Part I, by Leo G. Hertlein and A. M. Strong (2 plates); On the Electric Powers and Sex Ratios of Foetal *Narcine brasiliensis* (Olfers), by C. M. Breder, Jr., and Stewart Springer; A Study of the Activities of a Pair of *Galago senegalensis moholi* in Captivity, Including the Birth and Postnatal Development of Twins, by Florence De L. Lowther (6 plates); Diets for a Zoological Garden: Some Results During a Test Period of Five Years, by Herbert L. Ratcliffe; The Biology of the Smoky Shrew (*Sorex fumeus fumeus* Miller), by W. J. Hamilton, Jr. (4 plates, 1 text-figure); Social and Respiratory Behavior of Small Tarpon, by Arthur Shlaifer

and C. M. Breder, Jr. (2 plates, 1 text-figure); New Observations on the Blood Group Factors in Simiidi and Cercopithecidae, by P. B. Candela, A. S. Wiener and L. J. Goss; Muscle Dystrophy in Tree Kangaroos Associated with Feeding of Cod Liver Oil and Its Response to Alpha-Tocopherol, by Leonard J. Goss; Mortality Statistics for Specimens in the New York Aquarium, 1939, by Ross F. Nigrelli (3 plates); A Comparison of Some Electrical and Anatomical Characteristics of the Electric Eel, *Electrophorus electricus* (Linnaeus), by R. T. Cox, W. A. Rosenblith, Janice A. Cutler, R. S. Mathews, and C. W. Coates (7 text-figures).

AMERICAN WILD LIFE. *Illustrated.*

*Compiled by the Writers' Program of the Work Projects Administration in the City of New York. Wise and Company, New York.* $3.50. 9 x 5¾; xiv + 749; 1940.

The need for a greater appreciation and a wiser use of our natural resources has been the underlying stimulus for the preparation of this excellent volume. In its pages are found discussions on the appearances, the every-day habits, the economic value, the distribution, and the general life history of all the American chordates: i.e. mammals, birds, reptiles, amphibians, and fishes. The closing 243-page section on birds is especially good.

With the backing of the Works Progress Administration, the finished product incorporates the contributions of some fifty authorities on American natural history, and as a result, exhibits a high degree of scientific accuracy. The work is profusely illustrated, and is written in clear, non-technical language. It will undoubtedly be read and enjoyed by the general reader, as well as boys and girls of camp age.

ORNITHOLOGY LABORATORY NOTEBOOK. *For Recording Observations Made in the Field and Studies Made in the Laboratory on the Birds of North America. Fourth Edition.*

*By Arthur A. Allen, with Drawings by L. A. Fuertes, M. D. Pirnie, and William Montagna. Comstock Publishing Company, Ithaca, New York.* $3.00. 10½ x 7¼; vii + 204 + [32 unnumbered]; 1941.

The increased demand for a laboratory book on bird study has required the expansion of the material to render it useful to the whole United States. In this fourth edition the keys now include all orders and families of North American birds. Outline drawings of typical species are provided for the student to color, as well as outline maps for distributional data. Also in this notebook is an illustrated key to birds' nests, check lists for field trips, and Merriam's Life Zone map.

ENTOMOLOGICAL NOMENCLATURE AND LITERATURE.

*By W. J. Chamberlin. Edwards Brothers, Ann Arbor, Michigan.* $2.60 (cloth) $2.00 (paper). 10¾ x 8; ix + 103; 1941.

Part I of this volume presents a comprehensive history of entomological nomenclature from Aristotle, through Linnaeus and Say, down to the present International Congress of Zoology. The rules regulating the naming of new species are quoted and discussed for the benefit of new and inexperienced writers in the field of taxonomic entomology. Part II deals with the methods of assembling, filing, and the writing up of bibliographic material. This section includes also a comprehensive list of outstanding reviews, bulletins, journals, and textbooks in the general field of entomology.

THE PROBLEMS OF INSECT STUDY. *Second Edition.*

*By Paul Knight. Edwards Brothers, Inc., Ann Arbor, Michigan.* $2.50. 10¾ x 6¼; vii + 132; 1939 (paper).

The writer states that there is nothing in this text that has not been published before. It is primarily an introductory course in entomology, based on the questions asked by a diversified group of students. For this reason many different topics are included, such as the relationship existing between plants, insects, and man; feeding, growth and embryology; adaptations of insects; distributions and

economic importance; scientific control and legislative control; the plagues and diseases due primarily to insect infestation.

A table of scientific and common names of the more numerous insects, a short bibliography, and an index are appended.

A Field Key to Our Common Birds. *Pocket Natural History No. 8. Zoological Series No. 3.*

*By Irene T. Rorimer. Cleveland Museum of Natural History, Cleveland, Ohio.* $1.50. $6\frac{3}{4}$ x $3\frac{7}{8}$; 160; 1940.

This little guide to the common birds of the north Ohio area differs from most field books in that the birds are classified according to habitats. It is doubtful whether this method is superior to the usual systematic one as birds are very often where they should not be and it is sometimes difficult to decide just in what type of territory one is observing. However, there is a field key to the species, followed by numerous small illustrations drawn by Roger T. Peterson. Verbal descriptions of the species and an appendix of uncommon birds complete this pocket size edition that can be used throughout the northeastern United States.

Quetzal Quest. *The Story of the Capture of the Quetzal, the Sacred Bird of the Aztecs and the Mayas.*

*By V. Wolfgang von Hagen and Quail Hawkins. Harcourt, Brace and Company, New York.* $2.00. $9\frac{1}{4}$ x 7; 198; 1939.

The quetzal is the bird held in awe by the natives of Central America because of its relation to Quetzalcoatl. Its historical and mythological interest initiated the present attempt to bring this bird back alive, a feat never before accomplished. In an extremely lucid style—the book is written for children as well as adults—the quest for the quetzal is described. The capture of the birds, and their successful rearing and transportation was due in great part to a twelve-year-old Indian boy whose keen interest in the hunt rewarded him more than anyone ever expected. The pen-and-ink drawings are excellent.

Laboratory Manual for Introductory Invertebrate Zoology.

*By C. Courson Zeliff. The Evangelical Press, Harrisburg, Pennsylvania.* $1.00. (Obtainable from The Athletic Store, State College, Pa.). $8\frac{3}{4}$ x $5\frac{1}{2}$; 55; 1941 (paper).

The outline of this manual is broad enough to meet the needs of a variety of introductory courses in invertebrate zoology. The directions generally call for drawings of the external and internal anatomy of the organism; some require cross or sagittal sections to show internal relationships; and some include detailed studies of separate parts or appendages. A note on taxonomy and terminology, and a list of references have been included.

The Tale of the Bullfrog.

*By Henry B. Kane. Alfred A. Knopf, New York.* $1.25. 9 x $6\frac{7}{8}$; [47 unnumbered]; 1941.

The author has furnished not only the text but also the excellent photographs and the amusing pen and ink sketches for this delightful biography of a tadpole that grew up to be a bullfrog. Parents, as well as their children, will enjoy this book.

A Biogeographical Study of the Ordinoides Artenkreis of Garter Snakes (Genus Thamnophis). *University of California Publications in Zoology, Volume 44, No. 1.*

*By Henry S. Fitch. University of California Press, Berkeley and Los Angeles.* $10\frac{1}{4}$ x $6\frac{1}{2}$; 133 + 7 plates; 1940 (paper).

A Field Study of the Growth and Behavior of the Fence Lizard. *University of California Publications in Zoology, Volume 44, No. 2.*

*By Henry S. Fitch. University of California Press, Berkeley and Los Angeles.* $10\frac{1}{4}$ x $6\frac{1}{4}$; 22; 1940 (paper).

NOTES ON MEXICAN SNAKES OF THE GENUS GEOPHIS. *Smithsonian Miscellaneous Collections, Volume 99, Number 19.*

*By Hobart M. Smith. Smithsonian Institution, Washington, D. C.* 10 cents. 9½ x 6¼; 6; 1941 (paper).

FURTHER NOTES ON MEXICAN SNAKES OF THE GENUS SALVADORA. *Smithsonian Miscellaneous Collections*, Volume 99, Number 20.

*By Hobart M. Smith. Smithsonian Institution, Washington, D. C.* 10 cents. 9½ x 6¼; 12; 1941 (paper).

## BOTANY

THE ADVANCE OF THE FUNGI.

*By E. C. Large. Henry Holt and Company, New York.* $4.00. 8⅝ x 5½; 488; 1940.

In 1845 the potato Murrain destroyed the staple food crop of Ireland and spread "faster than cholera amongst men" throughout the British Isles and the potato growing countries of Europe. Nearly a century later, in 1939, Blight-proof potatoes were exhibited at the Royal Horticultural Society at Chelsea. Between these two events other food crop disasters occurred throughout the world. The Phylloxera of the vines caused such destruction in France in 1865–1872 that only the remaking of vines with root-stocks from America saved the French wine industry. The leaf rust put an end to coffee growing in Ceylon in the early '70s. In 1877 the *Saprolegnia ferax* disease spread into most of the salmon rivers of England almost as rapidly as did the potato Blight in Ireland 32 years before, and caused "consternation among gentlemen, fishwardens and gillies." These are but four of the more spectacular epidemics of fungus diseases told about in this fascinating book.

Although interest in the fungi had begun earlier the studies were mainly concerned with nomenclature and taxonomic relationships. It was the disasters of "the famished forties" and the controversy over whether Murrain was the cause or the effect of something else, that gave impetus to the development of the science of mycology and the research for effective fungicides. *The Advance of the Fungi* traces the discoveries in the identification of the various fungi, their life cycles, modes of transmission of plant disease, methods of control or eradication, and the personalities, both forgotten and illustrious, who contributed to our knowledge of plant pathology and epidemiology of fungus disease, and developed the science of crop defense.

The book is not only authoritative but is beautifully and wittily written. It is popular science at its best. The use of material from original scientific publications and contemporary accounts in newspapers and journals adds zest rather than dullness. The bibliography covers 26 pages, and there is an index.

PLANTS USED AS CURATIVES *by Certain Southeastern Tribes.*

*By Lyda A. Taylor. Botanical Museum of Harvard University, Cambridge.* $2.00. 10½ x 7; xi + 88; 1940 (paper).

Whether or not Indian herbal remedies are of any medicinal value has long been a debated question and there has been little published to substantiate either side of the argument. The present work is an attempt to analyze certain of these Indian remedies in the light of our knowledge of the medicinal properties of plants. Using the author's field material, gathered from two tribes, the Choctaw and the Koasati, and supplementing it with published literature, a fairly representative group of medicines for the southeastern United States has been here assembled. The material has been organized from a botanical viewpoint with the remedies listed by family, genera and species. The most recently accepted form of plant names has been used. Under each plant is listed the tribe or tribes using it, what it is used for, the part of the plant employed, and the method of preparing and applying it. The volume also contains a discussion of the plant data assembled, a glossary of the

terms used, charts illustrating the uses of the plants, a bibliography, and a complete index.

GERMAN FORESTS. *Treasures of a Nation. By Adalbert Ebner. German Library of Information, New York.* Free. 10 x 8¼; 127; 1940.

The author is Professor of Forestry at the University of Munich and Director of the World Forestry Institute. Forestry as a science and economic enterprise originated in Germany, and in this book Ebner traces its development. He tells how the different methods of silviculture have evolved and then rejected in favor of Gayer's new theory. This theory, which has gained world-wide application, is based on the establishment of small groups of trees in mixed stands of different ages, with the idea that regeneration of a stand should be achieved by natural reproduction rather than by artificial methods. The author continues with a discussion of all phases of German forestry, including the philosophy as well as the facts.

Excerpts from German poetry and 91 beautiful photographs taken by the author add interest and beauty to this book.

A MANUAL OF AQUATIC PLANTS. *First Edition. By Norman C. Fassett. McGraw-Hill Book Company, New York and London.* $4.00. 9 x 5¾; vii + 382; 1940.

Aquatic plants as defined by Fassett for his purposes, are plants that may, under normal conditions, germinate and grow with at least their base in the water and are large enough to be seen with the naked eye. It is not always possible to draw a distinct line between aquatic and non-aquatic plants. A lake or river that has been at low level for some time may suddenly rise, and plants will be found in its waters that would not ordinarily be defined as aquatics. Plants growing in bogs, small woodland brooks, waterfalls, tidal, salt and brackish waters are not included in the author's list, which, he admits, is highly subjective. The range covered is from Minnesota to Missouri eastward, and to the Gulf of St. Lawrence and Virginia. However, by no means all of the Virginia aquatics are included since Fernald is now at work on these, especially plants from the southeastern region.

An important feature of the book is the finely executed illustrations which occur on almost every page. The text is "essentially a set of directions for looking at the pictures." Part I (general key) "is based as far as possible on superficial characters for the identification of sterile specimens, and by it a plant may be run to species or genus or to family. . . ". Part II contains the descriptive treatment. In an appendix is given information on the uses of aquatic plants by birds and mammals, the relation of plants to fish, and a lengthy bibliography. The volume concludes with a glossary and a well-planned index. A highly useful book for those working in this field.

PLANTS AND MAN. *By Clarence J. Hylander and Oran B. Stanley. The Blakiston Company, Philadelphia.* $3.00. 8⅜ x 5⅝; x + 518; 1941.

This textbook presents a survey of botany as a vital, cultural, and practical subject. Its appeal is to the general interest of the average college freshman. Its aim is to develop in students an appreciation of the importance of plants and plant products to human affairs. It provides material for a semester's course in plant science, and builds a substantial foundation for further study in botany. Clearly written, abundantly and appropriately illustrated, and well organized, the volume is divided into the following general headings: Nature of the plant world, Plants as foods and beverages, Plants as sources of wood and fibers, Plant secretions and excretions, Plants as parasites, and Enjoyment of plant life. There is no bibliography, but

a complete glossary and index are provided.

A KEY TO WOODY PLANTS *Based upon the Flora of Itasca Park, Minnesota.*

*By Murray F. Buell and Robert L. Cain. Burgess Publishing Company, Minneapolis, Minn.* $1.00. $10\frac{7}{8}$ x $8\frac{1}{4}$; i + 30; 1940 (paper).

The detail and precision with which this key has been prepared make it a worthy contribution to the list of floral catalogues. The fact that the work is based on the trees and shrubs of Itasca Park, Minnesota, somewhat limits its range of usefulness, though it will serve well as a pattern for the preparation of keys relating to other local areas. The descriptions throughout are based on binary separations, each group being identified by the use of the same term: e.g., page 7, "c. Spines or prickles absent. . . . c. Spines or prickles present." A glossary and a check list of species included in the key are appended.

LIST OF SHRUBS EXCLUSIVE OF CONIFERS GROWING OUTDOORS IN THE BROOKLYN BOTANIC GARDEN 1940. *Guide No. 11. Brooklyn Botanic Garden Record, Vol. XXX, No. 1, 1941.*

*By Charles F. Doney. Brooklyn Botanic Garden Record, Brooklyn, New York.* 25 cents. 9 x $5\frac{7}{8}$; 35 + 5 plates; 1941 (paper).

Eighty-three families, 265 genera, 1021 species and 230 varieties, not including horticultural varieties of lilac and rose, are included in this list. Rehder's names have been used except in a few cases where old established names have been given with Rehder's new names in parentheses. There is an index of genera and common names.

## MORPHOLOGY

EMBRYOLOGY OF INSECTS AND MYRIAPODS. *The Developmental History of Insects, Centipedes, and Millepedes from Egg Deposition to Hatching. First Edition.*

*By Oskar A. Johannsen and Ferdinand H. Butt. McGraw-Hill Book Company, Inc., New York and London.* $5.00. 9 x $5\frac{3}{4}$; xi + 462; 1941.

Insect embryology has been so recently recognized as a distinct field of investigation, and the pertinent literature on the subject has been so scattered, that there has been a real need for a text wherein the basic principles, experimental techniques, and recent researches in the field could be incorporated into an organized entity. The present volume, dealing exclusively with the developmental history of insects, centipedes, and millepedes, from the time of egg deposition to hatching, fulfills this need.

The textual material, which is drawn largely from the authors' course in insect embryology given at Cornell, is presented under two general headings: I. A comparative study of the tissues and organs found in several basic types of insects; and II. The embryonic history of a number of insects so selected as to represent most of the orders. Under the first heading are included discussions on a variety of topics, such as types of eggs, cleavage, development, derivatives of the germ layers, polyembryony, parthenogenesis, and experimental embryology—the last mentioned incorporating the most recent authoritative studies on the activation and differentiation centers of the insect embryo. In dealing with the various orders of insects in Part II, the authors have been especially careful to avoid repetition of any of the material included in the preceding part.

The text is written with scientific clarity and simplicity, and is well supplied with illustrative material. Each chapter carries a list of references pertinent to the topic under discussion. Appended are a 36-page bibliography and a useful index.

THE GROWTH OF BONE, MUSCLE AND OVERLYING TISSUES AS REVEALED BY STUDIES OF ROENTGENOGRAMS OF THE LEG AREA. *Studies from The Center for Research in Child Health and Development, School of Public*

*Health, Harvard University, III. Monographs of the Society for Research in Child Development, Volume V, No. 3 (Serial No. 26).*

*By Harold C. Stuart, Penelope Hill, and Constance Shaw. Society for Research in Child Development, National Research Council, Washington, D. C.* $1.25. $8\frac{7}{8}$ x $5\frac{3}{4}$; vii + 190 + [29]; 1940 (paper).

The purpose of this study was to determine the manner in which children develop in respect to the rate and the amount of growth of bone, muscle, and subcutaneous tissue, and to the variability of these two factors during the early years of life. The study was based on a series of roentgenograms of the antero-posterior view of the right leg of a group of 85 boys and 88 girls. These films were taken at specified age intervals. The techniques used in taking, measuring, and weighing of the films are described in full. The early chapters are concerned with the norms obtained from the group as a whole and the last chapter presents examples of different types of individual growth patterns. In the case studies given, family background and social, dietary, and health factors are considered briefly in relation to the principal characteristics of the growth patterns revealed. There is a bibliography but no index. The appendix contains numerous tables presenting data pertinent to the study.

A Bibliography of Human Morphology 1914–1939.

*By Wilton M. Krogman. University of Chicago Press, Chicago.* $3.00. 11 x $8\frac{3}{8}$; xxxi + 385; 1941 (paper).

This bibliography of over eleven thousand titles deals chiefly with physical anthropology of the last quarter of a century, and as such is indispensable to all students of the human body. The author has performed an enormous and useful task in listing the work of others so that present and future students will know what information has become available and where to find it. One wonders, however, whether the bibliography of any large field of science can to-day still be collected and arranged to general satisfaction by one man alone. If the author of the present work had called on colleagues with different interests and experiences in physical anthropology, they could have supplied the many references now omitted, could frequently have assigned titles to more appropriate sections, and, particularly could have suggested essential changes in the Outline of Contents. Last but not least, several minds, instead of only one, could more readily have eliminated the all too many minor errors which have survived proof-reading.

This bibliography, even though incomplete, may well serve as proud evidence of the astounding productivity and widespread, active interest in the morphology of man during the recent history of anthropology. It probably equals in extent the entire corresponding literature previous to 1914.

The Embryology of the Echiuroid Worm Urechis caupo. *Memoirs of the American Philosophical Society Held at Philadelphia for Promoting Useful Knowledge, Volume XVI.*

*By William W. Newby. American Philosophical Society, Philadelphia.* $2.00. $9\frac{1}{8}$ x 6; xvi + 219; 1940.

The author of this fine treatise discusses first the reproductive system and germ cells of *Urechis* and the material and methods used in the embryological investigations. In the section on the development of *Urechis* the nomenclature of cell-lineage, as modified by Conklin in 1897, is briefly explained and the zygote is carried through to the 148-cell stage. This is followed by a presentation of gastrulation and shifting of embryonic areas and axes. Finally the individual development of the various organ systems is shown. The latter half of the book is concerned with a comparison of the development of *Urechis* and that of other Echiuroidea, and a comparison of echiuroid development with the embryology of several other invertebrates. In the final section there is a discussion of the phylogenetic position of the Echiuroidea based upon embryonic characteristics.

The author concludes that echiuroids are only distantly related to the annelids. He recommends, therefore, that the Echiuroidea should be considered a separate phylum and not placed as a subphylum or class under the Annelida.

Eighty-five excellent figures, 4 tables of cell-lineage, a bibliography of 50 titles and a good index have been provided.

ENTWICKLUNGSGESCHICHTE DES MENSCHEN. *Zweite, neubearbeitete und erweiterte Auflage.* *By Max Clara. Quelle und Meyer, Leipzig.* RM. 13.60 (25 per cent discount outside of Germany). $8\frac{3}{4}$ x $5\frac{1}{2}$; xv + 550; 1940.

The completeness of this book makes its possession well worth while to students of human embryology. Many illustrations add to its teaching value. The heredity, spermatogenesis and oogenesis, and embryology of the frog are used as an introduction to the more complicated subject of human embryology.

The first division of the volume deals with the structure of the sex cells, fertilization, and the rôle of sex in inheritance; the second treats extra embryonic membranes, gastrulation, and processes of placentation, and the formation of ectoderm, endoderm and mesoderm; the third concerns the development of organs and organ systems.

A large bibliography is appended, and there is an index.

THE MALE GENITALIA OF HYMENOPTERA. *Smithsonian Miscellaneous Collections*, Volume 99, Number 14.

*By R. E. Snodgrass. Smithsonian Institution, Washington, D. C.* 40 cents. $9\frac{1}{2}$ x $6\frac{1}{4}$; 86 + 33 plates; 1941 (paper).

## PHYSIOLOGY AND PATHOLOGY

MAN ON HIS NATURE. *The Gifford Lectures, Edinburgh 1937–8.*

*By Sir Charles Sherrington. The University Press, Cambridge; The Macmillan Company, New York.* $3.75. $8\frac{3}{8}$ x $5\frac{1}{2}$; 413; 1941.

This book, by the distinguished physiologist and recipient of the Nobel Prize for Medicine in 1932, was written for the Gifford Lectures, 1936–38, at the University of Edinburgh. It is a discussion of man's nature, its physiological basis, and its evolution. Sherrington takes for his text the book *On Hidden Causes* (*De Abditis Rerum Causis*) by Jean Fernel, physician to Henri II of France. Cast in dialogue form this treatise, first published in 1548, was within the next hundred years reissued more than thirty times and in several countries. Living in a period when magic, astrology, elixir-brewing, the philosopher's stone and the cabala all had a profound influence on human thought and behavior, Fernel's virile mind perceived that there was order and balance in nature.

". . . misbalance in constitution is the illness, yet the cause is the practical point. There are causes we do not know" and again "Each animal, each plant, each mineral, whatever is in this sub-lunary world, contains a particular Nature which maintains and orders it and its kind. This particular Nature, unalterable as it is, fits with all other particular Natures." Fernel was "the earliest to draw together into one discipline physiology, calling it for the first time by that name, and holding it to be the necessary introduction to scientific medicine."

Sherrington gives a clear-cut and extremely interesting picture of the development of modern biological knowledge and the part that physics and chemistry have had in that development. Fernel's questions in the "Dialogues" he answers in the light of modern knowledge. Most of the questions are discussed in terms of the central nervous system. Concerning the problems raised by the reappearance of the mind *ex nihilo* at each repetition of the soma after the soma has reached a certain stage of ripeness, and the difficulty of interpreting mental phenomena in terms of physics and chemistry, Sherrington says:

We have, it seems to me, to admit that energy and mind are phenomena of two categories. In that case the phasic appearance of a mental system alongside the energy-system of the developing body has the difficulty that the mental seems to spring suddenly out of nothing. But we have already dealt with

instances in ourselves where mind is clearly inferable although not directly recognizable by us. If that be so in ourselves, still greater is the difficulty of observing mind objectively, that is as object, when, by its very nature, it is insensible, i.e. not accessible to 'sense'. Mind as attaching to any unicellular life would seem to me to be unrecognizable to observation; but I would not feel that permits me to affirm it is not there. . . .

The appearance of recognizable mind in the soma would then be not a creation *de novo* but a development of mind from unrecognizable into recognizable. It is at this point therefore that on these admissions we become committed to dualism. But while accepting this duality we remember that Nature in instance after instance dealing with this duality treats it as a unity. Evolution evolves it as one. In this body-mind individual, with its two cohering systems, bodily and mental, even as the former component exhibits both inherited and acquired features, so too does the latter.

With biologists becoming concerned with smaller and smaller values, it is refreshing to read the broader philosophy of such an outstanding physiologist. The volume is well printed, has a combined subject and author index and has beautifully designed title pages to each chapter. We strongly recommend this book as seminar work for graduate biology students. It lends itself admirably to discussion groups.

PHYSIOLOGIE DES SEHENS. *Retinale Primärprozesse.* *By G. von Studnitz. Akademische Verlagsgesellschaft, Leipzig.* RM. 24 (cloth); RM. 22 (paper). 8⅜ x 5½; xii + 367; 1940.

Modern students of the physiology of vision have approached the problem from such diverse and widely separated points of view that no one worker or group of workers in this field can be said to command authority in the whole subject. Some appreciation of the diversity of the approaches to this problem may be obtained by simply listing the most important fields of study. There are, first, anatomical investigations concerning the structure of the light sensitive end organs and the neuroanatomy of the retina. This field has been extended into the submicroscopic region in respect to the retinal end organs by polarization microscopy and studies on optical dichroism—techniques not regularly found in the anatomical laboratory. Far removed from these anatomical studies are those of neurophysiologists on the electrical responses of the excited retina. Here is a field of great complexity that has been diligently cultivated by a large number of workers. Equally removed from anatomical and neurophysiological techniques are those of the biologists and biochemists bent in isolating the photochemical substances primarily concerned in the response of the retina to light, and in discovering the metabolic processes by which these photochemical substances are produced. Finally, there is a large group of psychologists, ophthalmologists, and others who have studied the subjective sensory aspects of visual perception and who provide, in a sense, the raw material which the other workers attempt to explain and understand.

The centrifugal aspects of this field of science are, of course, not unique. In very many other fields similar trends have long been manifest. The conventional cure for this condition is either the organization of an institute, the creation of a commission, or the composition of a monograph. Von Studnitz has provided a workmanlike example of the third form—a monograph in which the four major fields of attack on the physiology of vision are discussed and in some respects co-ordinated. There is an excellent bibliography indicating that the subject has been competently covered.

The author's own investigations have concerned the photochemical substances of the retina. Here he exhibits himself in violent and polemical disagreement with his nearest colleagues.. The reviewer does not feel competent to render a verdict on the points at issue but it is plain that the parenthetical sarcasms and abundant exclamation points, sometimes in pairs, which are scattered through this section of the book, do not add one cubit to the author's stature.

TEMPERATURE. *Its Measurement and Control in Science and Industry. Papers pre-*

*sented at a Symposium held in New York City, November, 1939.*

*Under the Auspices of the American Institute of Physics with the Cooperation of National Bureau of Standards and National Research Council. Reinhold Publishing Corporation, New York.* $11.00. 9 x 6; xiii + 1362; 1941.

This volume presents the papers given at a Symposium on Temperature held in New York City in 1939 under the auspices of the American Institute of Physics. The subjects covered range from the temperature of the stars to production and measurement of temperatures below 1°K. Unfortunately, it is not possible in a limited space to give the salient points in the papers dealing with purely biological problems, but we give the titles of some of these (they are all by American investigators) as an indication of the important work that is being done on the effect of heat and cold on living systems.

The temperature of the human body in health and disease; The resistance of living matter to very low temperatures; The development of homeothermy in animals; Heat production and thermal conductance in small laboratory animals at various temperatures; The effects upon dogs of low oxygen tensions combined with low temperatures; Temperature factors in animal production; The temperature pattern of laboratory animals in normal and febrile states; Temperature sense in man; A new basis for cutaneous temperature sensitivity; Man's heat exchanges with his thermal environment; The operating characteristics of the human thermoregulatory mechanism; Heat loss and heat production in women under basal conditions at temperatures from 23°C to 35°C.; The significance of the average temperature of the skin; Temperature changes in the muscles of the human leg; Skin temperature of the extremities under various environmental and physiological conditions; Normal vasoconstriction vasospasm and environmental temperature; Observations on human beings with cancer, maintained at reduced temperatures of 75°–90° Fahrenheit.

Tabular matter, graphs, and references are included in each paper. The book has an author index and subject index and a valuable appendix giving the constants used in thermometry.

AUTHORITY, OBSERVATION AND EXPERIMENT IN MEDICINE. *Linacre Lecture 1940. By W. W. C. Topley. The University Press, Cambridge; The Macmillan Company, New York.* 40 cents. 7¼ x 4⅞; 46; 1940 (paper).

In the Linacre Lecture of 1940, Topley disagrees with two of his predecessors in the unqualified praise which they bestow upon Linacre. Galen's ideas that had dominated medicine for thirteen hundred years were being replaced early in the sixteenth century by revolutionary changes of which Linacre was unaware. His translation of Galen's Greek writings into admirable Latin, to replace the corrupt versions, was a great medical achievement, but, Topley says, it can also be cited as an example of doing the wrong thing extremely well. Other men of Linacre's time were aware of the beginning of a new order in medicine. It is said that Paracelsus inaugurated his professorship at Basel, in 1527, by publicly burning the works of Galen and Avicenna. The following quotations will serve to give the reader some idea of Topley's views.

"Linacre the physician must, I think, be numbered among the authoritarians; and authority—the intellectual authority of books or men—is incompatible with science. The scientist can never regard his books as more than temporary codifications of current working hypotheses, and of the evidence on which they are based. All books, and all men, remain open to challenge, and there can be no plea of privilege.

"Medicine is not a self-sufficing entity. It is, as we know it to-day, the application to the cure and prevention of disease of knowledge and of methods drawn from a wide variety of ancillary sciences—ancillary, be it noted, only in the sense that they have services to offer to medicine, . . .

"If we could kill the last remnants of authoritarianism, abolish the false distinction between the medical scientist and the medical artist, and gain general acceptance for the view that controlled observation in the ward or in the field is an essential part of medical science, shading through almost imperceptible stages of increasing intervention into the fully developed experimental technique of the laboratory, we should, I am sure, have gone a long way to secure the intellectual sympathy and understanding that is the essential basis of fruitful common effort."

A HISTORY OF MEDICINE. *By Arturo Castiglioni. Translated from the Italian and Edited by E. B. Krumbhaar. Alfred A. Knopf, New York.* $8.50. 9¼ x 6¼; xxviii + 1013 + xl; 1941.

Confronted by a truly monumental treatise

prepared by one of the most eminent student's of the subject, it is difficult to condense within the brief space allotted the considerations which this work deserves. For Castiglioni not only delineates the development of the medical art and science but he also reveals the relation of this development to that of philosophy, science in general, and social and economic policies and ideas. Thus, the status of medicine in a certain period is made to reflect the intellectual and moral characteristics of that period. This is one of the most distinctive features of the present work. The whole recorded existence of man is covered, from the prehistoric indications of the practice of some kind of surgery to the latest discoveries concerning etiology, therapy, and prevention of disease. With respect to the medicine and surgery of our era, the author duly mentions all the well-known contemporary personalities but with a just regard for historical values he withholds comments on them. The author attributes more importance than is usually given by English students to the medical contributions of Italian physicians. To some this may seem a manifestation of chauvinism, but even though in certain cases the author's evaluation may be slightly prejudiced, it leads to a clearer conception of the evolution and dissemination of ideas more or less simultaneously in different groups. One of the noteworthy reflections made by the author concerns the evaluation of ancient Roman medicine. The author points out that, since the public hygiene and sanitation of Rome and other cities of the empire achieved a standard not equalled until modern times, it cannot be very well affirmed that Roman medicine consisted only of a pedestrian imitation of that of Greece! From the standpoint of medical science and of history this textbook undoubtedly deserves a place with the leading works on the subject.

PLAGUE ON US.

*By Geddes Smith. The Commonwealth Fund, New York; Oxford University Press, London.* $3.00. 9 x 5¾; 365; 1941.

During recent years the popularity of books that portray to the layman the advance of medical science is evidenced by the number of such publications. Many of them present the story in such dramatic style that there is some distortion of scientific perspective—personalities may be allowed to overshadow science. Such is not the case with this book, of which only the title may convey such an impression. It is a relief to read the story as it is here presented with good taste, balanced judgment and objectivity. Scientists are depicted neither as heroes nor as eccentric individuals; in fact, they are presented only as discoverers and authors.

There are seven chapters, a prologue and an epilogue. These chapters are: Pestilence, in which the problems are defined from an historical viewpoint; Past Thinking, in which is traced the development of ideas regarding the nature of contagion and infection; The Sick Man, considering the inter-relations of parasite and host; The Sick Crowd, epidemiological studies; Defenses, individual and collective; Detective Work, illustrations of diagnostic bacteriology and epidemiology in action; Unfinished Business, in which it is shown that notwithstanding the progress which has been made, much more remains to be accomplished.

The author exhibits an admirable ability to present scientific material in an interesting and understandable manner without sacrifice of accuracy and without resort to sensationalism. If, as the author modestly states, he has been much aided by the advice and criticism of friends, his friends have been well chosen.

PHOTODYNAMIC ACTION AND DISEASES CAUSED BY LIGHT.

*By Harold F. Blum. Reinhold Publishing Corp., New York.* $6.00. 9 x 5¾; xii + 309; 1941.

Photodynamic action has interested many investigators since its discovery by Raab in 1893. One research worker some years ago concluded an admirable review with the remark that "there is little evidence that such sensitization plays any significant part either in the etiology or

therapy of the diseases of man." The present author, however, feels more confidence in the importance of the subject. Himself a contributor of many research papers dealing particularly with the rôle of oxygen in photodynamic action, the author devotes a major part of the first section of the book to a discussion of the factors determining photodynamic effectiveness. He also discusses at length the various theories proposed to account for the effect, although these are still in the nature of hypotheses. This material is interesting to the specialist who is actively working in this particular field.

The sections dealing with the diseases produced by light in domestic animals and in man are of more general interest. The fact that animals may become light sensitive as the result of feeding on St. Johnswort or buckwheat has long been known and frequently becomes a serious problem for the stock breeder. Sensitization of man has usually been attributed to the porphryms and this subject is discussed very thoroughly. There is also an analysis of the relation of light to skin cancer, a subject in which there is much current interest. The book is exceedingly readable and members of the medical profession will find much to interest them in the final section.

HYGIENE. *A Textbook for College Students on Physical and Mental Health from Personal and Public Aspects. Third Edition.*

*By Florence L. Meredith. The Blakiston Company, Philadelphia.* $3.50. 9 x 5¾; xii + 822; 1941.

This comprehensive volume incorporates discussions of human anatomy, physiology, pathology, group biology, and personal hygiene. The predominant theme is the appropriate scientific action which is necessary to meet the health objectives arising from the health situations which exist in the lives of individuals or groups. It is essentially a new book, having been completely revised in the light of the most recent medical developments.

The opening pages give a statistical survey of mortality and morbidity in the United States. Chapters on anatomy and physiology have been condensed from previous editions, but a valuable new section discusses the manner in which medical science may be used most effectively, warning against nostrums and quackery. Accidents and diseases, generally and specifically, are described in considerable detail, but the major portion of the volume is devoted to considerations of what the individual can do to maintain proper functioning of the various organs and organ systems. The book does not deal with general conditions of interest. It is complete and specific, written from the point of view of the physician. Although *Hygiene* is an excellent college textbook, it will find little use beyond academic doors.

THE PERIODICITY AND CAUSE OF CANCER, LEUKÆMIA AND ALLIED TUMOURS *with Chapters on Their Treatment.*

*By J. H. Douglas Webster. The Williams and Wilkins Company, Baltimore.* $3.50. 9½ x 6¼; xv + 178; 1940.

Periodicity in tumors was first mentioned by Bashford and co-workers in 1905. Since that time a number of others have found evidence that there are periods of quiescence in malignant tumors. The present studies, based on 720 cases (589 malignant cases, 42 leukaemia, 51 Hodgkin's disease, 38 benign tumors), were the result of the discovery that a patient had had breast cancer recurrences on five occasions at approximately 33-week intervals. Clinical and statistical evidence is given by Webster to show that periodicity is "a fundamental and intrinsic character of human neoplastic disease. . . ."

"The time-pattern which has been found is not a simple one (or it would have been discovered long ago); it has a triple *facies*, showing itself as full, half, or 'missed' periods; the standard full-period being 33 weeks, as in influenza."

It was found that treatments (surgery or radiotherapy) would postpone or abolish the appearance of the periodicity, but the rhythm was not altered. Webster believes that the periodicity of cancer and

the rare instances of contagion lend support to more direct evidence of the virus causation of tumors.

BIOLOGICAL ASPECTS OF INFECTIOUS DISEASE. *By F. M. Burnet. The University Press, Cambridge; The Macmillan Company, New York.* $3.75. 8½ x 5⅜; vii + [5] + 310; 1940.

The point of view from which the author discusses infectious diseases is that of the ecology of the pathogenic parasite. He seeks to make it clear that parasitic diseases represent certain kinds of reactions between man and other organisms, and that these organisms are subject to the same natural laws which regulate all living matter. In some detail the author describes first the kinds of parasites: bacteria, viruses, etc. He then proceeds to delineate the interaction between the parasite and man in terms of disease resistance and immunity, and epidemics. Separately, the author treats of some of the more important infectious diseases—diphtheria, influenza, tuberculosis, plague, cholera, malaria, and yellow fever—with an account of their etiology, incidence, and epidemiology. Although the book is apparently written for the non-biologist, it deserves to be read and pondered by all who are interested in medical sciences. An exception could be taken to the title since the author omits any but the most indirect mention of the biology of the host, man.

TEXTBOOK OF HEALTHFUL LIVING. *Second Edition. By Harold S. Diehl. McGraw-Hill Book Company, New York and London.* $2.75. 8⅞ x 5¾; x + 634; 1939.

In its original form the volume was written for the general reader. The carry-over of this method of presentation seems to limit the usefulness of the present edition as a textbook. Major topics discussed are the present situation regarding health and longevity, nutritional and digestive considerations in the maintenance of health, the relationship of the individual to his physical environment, and immunization. Somewhat more specific are chapters describing the care of teeth, throat, nose, ears, and eyes. General treatment is accorded to sex life, mental health, and diseases of advanced age, while the closing chapters discuss public health services. Very little space is given to anatomy or physiology, since the author considered these subjects as being "only remotely related to the practice of personal hygiene. . . ." This still remains a good book for the general reader, but will be most useful in college courses as a source of supplementary information. The volume contains many good references and is thoroughly indexed.

STUDIES ON TUBERCULOSIS. *The American Journal of Hygiene Monographic Series, No. 16, February, 1941.* Containing the following: *The Spread of Tuberculosis in Negro Families of Jamaica, B.W.I.*, by E. Joyce Saward, Persis Putnam, and Eugene L. Opie; *The Fate of Negro Persons of a Tropical Country, Jamaica, B.W.I., after Contact with Tuberculosis*, by Eugene L. Opie, Persis Putnam, and E. Joyce Saward; *A Survey of Tuberculosis Infection in a Rural Area of East Alabama*, by A. H. Graham, P. W. Auston, and Persis Putnam; *The Fate of Persons Exposed to Tuberculosis in White and Negro Families in a Rural Area of East Alabama*, by A. H. Graham, P. W. Auston, and Persis Putnam.

*The Johns Hopkins Press, Baltimore.* $1.10. 9 x 5¾; 198; 1941.

Although presented separately, these four papers are so closely interrelated that the volume is essentially a monograph. In general the authors conclude that tuberculosis runs a shorter, sharper course, and more frequently ends fatally in Negroes than among whites, and that there is a higher frequency of latent tuberculosis among whites. Data on the development of secondary cases in family groups after the removal of active cases from those groups are also presented. Two family

charts are given as illustrations at the end of the book.

MEDICINE AND HUMAN WELFARE.

*By Henry E. Sigerist. Yale University Press, New Haven; Oxford University Press, London.* $2.50. 8 x 5¼; xiii + 148; 1941.

One theme dominates the pages of this book: namely, that throughout history the medical treatment of the working classes has been inadequate. Sigerist describes the intimate relationship between medicine and social changes from earliest times, showing how we have come to accept the view that all classes are deserving of equal medical attention, and how at the same time we have neglected to carry out this policy. It is true that within recent years the socialization of medicine has progressed rapidly, but, according to Sigerist, it is limited by an adverse and inadequate economic system.

The book presents a broad health program for every country, one aspect of which must be the freedom of the physician from the sphere of competitive business. It is further emphasized that scientific medical research is not enough. It must be supplemented by sociological investigations.

FAMOUS RECIPES BY FAMOUS PEOPLE.

*Compiled and Edited by Herbert Cerwin. Illustrated by Sinclair Ross. Lane Publishing Co., San Francisco, California.* $1.00. 9 x 6½; 62; 1940.

Among the famous people who are contributors to this interesting recipe book are Julian Street, whose "spinach in coated pellets" may possibly make some friends for this unpopular vegetable; Kathleen Norris whose "crab Creole romantique" is more than *romantique;* Gertrude Stein, whose "chowder Alice B. Toklas" is as complicated to concoct as her writings are to comprehend; Irwin Cobb, whose "southern hash" is worthy of a banquet; and many chefs, whose dishes have made restaurants famous. However, the contribution which most takes our fancy is by the anthropologist and explorer Hrdlicka:

> The front quarter of a sheep, roasted slowly over hot embers, under a studded sky, in a semi-desert, with but a native or two about, and the mules or horses; with the night deepening around, the earth resting, and the worlds beginning to talk to each other.

DEUTSCHE WISSENSCHAFT IM KAMPF UM DIE HEILUNG DER TUBERKULOSE. *Vorschlag zur Gründung eines Deutschen Tbc.-Therapie-Forschungsinstitutes.*

*By Wilhelm Pfaff. Georg Thieme Verlag, Leipzig.* RM. 1.20 9¾ x 6⅜; 32; 1941 (paper).

In 1933 the author gave an account of his work on the care and cure of the tuberculous in a monograph *Der Aufbau der Tbc. Therapie als wissenschaftliches und staatliches Problem.* This is summarized briefly in the present study, and the results of further work reported. Some of his experiments on animals were unsuccessful and could not be carried out satisfactorily because systematic investigations in this direction needed a broader basis. The author therefore suggests the foundation of a German Therapeutic Research Institute for Tuberculosis, with four interdependent divisions: pharmacological, pathological-anatomical, bacteriological and hematologic-serological, and chemical. The duties and problems of the four divisions are outlined briefly.

MICROBIOLOGY AND PATHOLOGY. *Fifth Revised Edition.*

*By Charles G. Sinclair. F. A. Davis Company, Philadelphia.* $3.25. 8½ x 5½; ix + 393; 1940.

It seem particularly desirable to present bacteriology, the study of viruses, protozoology, mycology and parasitology in the form of one subject—microbiology. It is also desirable to relate pathology to microbiology. The present volume, an elementary text for nurses, dieticians, and for those engaged in physiotherapy and occupational aids, is of necessity broad in

scope. It therefore suffers from the difficulties that any book of this type encounters. However, the book is well planned and in spite of some inaccuracies due to over-simplification and the fact that the bacteriological terminology is archaic and inconsistent, it has fewer faults than others in the same field. The volume is well illustrated and is indexed.

How to Prevent Goiter.

*By Israel Bram. E. P. Dutton and Company, Inc., New York.* $2.00. 8 x 5⅛; 182; 1941.

It is estimated that over 7,000,000 Americans suffer from goiter and glandular diseases. In this volume a medical authority dispenses pertinent preventive information for the lay reader. The book is not offered in any way as a substitute for the physician. It is the purpose of the author to set forth the simple rules of physical and mental conduct that will help to prevent disturbances of the thyroid gland. He discusses in order: the rôle of the thyroid in life's processes; the healthy and unhealthy thyroid; causes and varieties of goiter; goiter "belts"; the prevention and treatment of simple and exophthalmic goiter; and the effects of eating, sleep, and thinking on the thyroid gland. The book is illustrated with representative cases. There is an index, but no bibliography.

The Comparative Physiology of Respiratory Mechanisms.

*By August Krogh. University of Pennsylvania Press, Philadelphia.* $3.00. 9 x 5¾; vii + 172; 1941.

This book presents the subject from the comparative viewpoint, and, therefore, is a valuable addition to our texts on respiration. The author has collected numerous facts concerning the respiratory activity of many types of animals and discusses their need for oxygen and their mechanism for meeting this need. Since a large amount of this work has been done by Krogh and his assistants, the book is mainly a first-hand account of these researches. It is an admirable presentation of the ability of animals to adapt their respiratory mechanisms to environments of air or water. The work contains a list of references, an index of animals mentioned in the text, and a subject index.

The Machinery of the Body. *Revised Edition.*

*By Anton J. Carlson and Victor Johnson. The University of Chicago Press, Chicago.* $4.00. 8⅞ x 6; xix + 620; 1941.

A revised edition of a popular college text on physiology. New material has been incorporated in the chapters already published and a new chapter on reproduction has been added. The clarity of presentation of the text and the excellence of the illustrations make this book valuable for college students desiring to understand the basic functions of the human body. There is a good subject index and a short list of selected references.

Die Geschichte der Schwindsucht.

*By Richard Bochalli. Georg Thieme Verlag, Leipzig.* RM. 4.80; RM. 3.60 (outside of Germany). 9½ x 6¼; 73; 1940 (paper).

Written primarily for medical students, this history of studies on, and theories concerning, phthisis and the treatment of patients, begins with pre-Hippocratic times and ends with the seventeenth century, i.e. Harvey, Paracelsus, Konrad Schneider, Malpighi, and their medical contemporaries. It is adequately annotated, and there is a bibliography but no index. A second part, to treat the history of pulmonary tuberculosis, is planned.

Spital und Artz von Einst bis Jetzt.

*By Richard Goldhahn. Ferdinand Enke Verlag, Stuttgart.* RM. 8 (cloth); RM.

6.40 (paper). 9⅞ x 6½; viii + 188; 1940 (paper).

A well-written, brief, and at times intentionally sketchy, history of the development of medical practice and hospital services from antiquity to the present day. An appendix discusses watering-places and bath cures. A fairly lengthy bibliography is arranged under various headings, such as Middle Ages, epidemics, modern times, treatment of the insane. Illustrations add interest to the volume.

## BIOCHEMISTRY

THE CHEMICAL ACTION OF ULTRAVIOLET RAYS.

*By Carleton Ellis and Alfred A. Wells. Revised and Enlarged Edition by Francis F. Heyroth. Reinhold Publishing Corporation, New York.* $12.00. 9 x 6; ix + 961; 1941.

The familiar work of Ellis and Wells, published under this title in 1925 by the Chemical Catalog Company, has been greatly enlarged in this revision and somewhat extended in scope. As the book in its original form is well known to workers in the field of photochemistry a comparison of the original text with the revised edition will perhaps give the clearest idea of the new text.

In the section on sources of ultraviolet radiation there is a new chapter on the emission of radiant energy which is a valuable addition, and there is also much new material on the carbon arc, solar radiation, and ultraviolet transmitting glasses and filters which makes the revised text a far more inclusive reference book than the earlier one. It seems unnecessary, however, to devote three chapters to details of the construction and operation of mercury vapor lamps. This material could have been condensed with advantage.

In the second section on photochemical processes there are several valuable new chapters on the mechanism of photochemical processes and a very inclusive summary of photochemical reactions. The great body of new material in this field since 1925 makes this section particularly interesting.

The section on applications of photochemistry to industrial products is largely new material as this topic was touched on only very briefly in the earlier text.

Like all the other sections the part on applications of ultraviolet radiation in biology has been very much expanded due, naturally, to the large volume of work that has been done in this field since 1925. While the chapter on the photochemical behavior of compounds of biological interest is very significant and most appropriate for inclusion it seems to the reviewer that this section as a whole could have been condensed with advantage by including only those biological effects of ultraviolet radiation which can be clearly related to definite photochemical changes. The author states that this was his intention but the material could have been more restricted with advantage.

The book will serve as a valuable reference work in photochemistry and the only criticism found is the fact that in an effort to make the material inclusive for workers in both chemistry and biology the author has made the book unwieldy in length. The new material added in Parts II and III is extremely important and much of it is not readily available elsewhere. The material in Parts I and IV that has been adequately reviewed in other publications might have been cut to a minimum with advantage. But the book as a whole will be very valuable to photochemists and more than fills the need for a revision of the earlier book which is now so completely out of date.

DIE METHODEN DER FERMENTFORSCHUNG. *Lieferung 5.*

*Edited by Eugen Bamann and Karl Myrbäck. Georg Thieme Verlag, Leipzig.* RM. 42. 11 x 8; 1277–1836; 1940 (paper).

A further contribution (cf. Vol. 15, p. 503 and Vol. 16, p. 239 for notices of the earlier numbers) to a comprehensive series on methods of enzyme investigation presented by some of the foremost workers in their field. In the present number Part I of the entire study is concluded and Part II begun. The continuation of Part I presents: (a) general methods of preparing

algae, yeasts, molds, protozoa, embryonal tissues, and adult tissues for enzyme analysis; (b) general methods of enrichment and separation of enzymes, chromatography, foam analysis, and electrophoresis; (c) methods for determination of the more general characteristics of biological catalysts. The effect of radiation and heavy water on fermentation are also discussed. In the section of Part II included in this number more particular attention is paid to the preparation, analysis, and properties of the purified hydrolases and carbohydrases. Unfortunately, the bibliography will not appear until the end of the completed series.

THE BIOCHEMISTRY OF SYMBIOTIC NITROGEN FIXATION.

*By Perry W. Wilson. The University of Wisconsin Press, Madison.* $3.50. 9 x 5½; xiv + 302; 1940.

This monograph has been prepared as a sequel to *The Root Nodule Bacteria and Leguminous Plants* by E. B. Fred, I. L. Baldwin, and Elizabeth McCoy, published in 1932. At that time "the chemistry of symbiotic nitrogen fixation was a relatively unexplored field." The present volume presents in a readable manner the extensive studies the author and others have contributed to the subject since the publication of the earlier one. It gives a broad chemical approach to the knowledge of the Leguminosae and the complex relationship existing between symbiotic bacteria and plants, including the relevant vitamin complexes, bacteriophage, auxins, photochemistry, secretory mechanisms, the $pN_2$ and $pO_2$ functions, and isotope tracer results. An up-to-date cross-indexed bibliography completes this book, which should prove useful to biologists and agriculturists as well as to workers in the specific field.

IF THEY COULD SPEAK!

*Chilean Nitrate Educational Bureau, 120 Broadway, New York.* Free. 7¾ x 5¼; 56; 1941 (paper).

Ninety-five kodachrome illustrations, showing results of mineral deficiency (boron, calcium, copper, iron, magnesium, manganese, nitrogen, potash, and zinc) in 34 grains, vegetables or fruits, make up this little book. Each plate is accompanied by a descriptive identification.

It is suggested that the correct use of such natural fertilizer materials as Chilean nitrate of soda, which contains these necessary elements as impurities, will prevent the development of plant food-deficiency diseases. It is not claimed, however, that it is a cure-all which will promptly correct a deep-rooted condition resulting from long neglect.

WHAT ARE THE VITAMINS?

*By Walter H. Eddy. Reinhold Publishing Corp., New York.* $2.50. 9 x 6; [8] + 247; 1941.

Today everyone is conscious of the importance of vitamins, but few people have a reliable knowledge concerning them. The content of this book answers the query in the title. A brief history of the subject is followed by a discussion of the probable function of vitamins as necessary factors in cellular respiration and metabolism of specific tissues. In succeeding chapters the vitamins are dealt with letter after letter as to the physiological manifestations of deficiency consequent upon histological changes. In each case methods are explained for diagnosing the deficiency, and the normal requirements are given when known. The author reviews the most authoritative literature on each subject, presenting an extensive bibliography. In the appendix the chemical composition and properties of vitamins are given, and also a table of vitamin units, by weight and portion, found in foods. For biologists and physicians the book will be highly useful, but the specialized medical and chemical terminology will preclude any service to the masses.

MECHANISMS OF BIOLOGICAL OXIDATIONS.

*By David E. Green. The University*

*Press, Cambridge; The Macmillan Company, New York.* $2.75. 8½ x 5¼; 181; 1940.

This compact volume is a welcome change from the lengthy presentations that are so often characteristic of enzyme literature. In a concise and systematic manner the author presents the most recent facts and interpretations of enzymatic oxidations, particularly of those systems where the pure enzymes or prosthetic fragments have been used in the studies. The prosthetic groups containing copper, iron, zinc, flavin, nicotinicamide, thiamine, and glutathione are particularly discussed. References are provided with each chapter and there is an index. A stimulating, clearly-written book for thinkers in this field.

THE THEORY OF ORGANIC CHEMISTRY. *An Advanced Course.*

*By Gerald E. K. Branch and Melvin Calvin. Prentice-Hall, New York.* $4.00. 9 x 5¾; xix + 523; 1941.

A good fundamental and methodological approach to theoretical organic chemistry, presenting the most basic concepts of classical structural chemistry, of physics, and wave mechanics. The authors, realizing the state of flux of modern chemical concepts have presented their own views on the subject, and confined other views for the mechanisms discussed to very brief treatment. The nomenclature used is that felt by the authors to be the most clear and permanent. Advanced students of organic chemistry and molecular structure will find this book well worth reading.

PHOTOSYNTHESIS.

*By E. C. C. Baly. D. Van Nostrand Company, New York.* $4.75. 8½ x 5¼; vii + 248; 1941.

After describing the more important characteristics of photosynthesis, the author presents a detailed account of investigations of this process carried on in his own laboratory. The author believes that his investigations have led in the end to the photosynthesis in the laboratory of carbohydrates from carbon dioxide and water. Although careful workers here and abroad have not been able to confirm this feature of Baly's work, his own account of his experiments will interest students of photosynthesis.

MAGIC IN A BOTTLE.

*By Milton Silverman. The Macmillan Company, New York.* $2.50. 8⅜ x 5⅜; xi + 332; 1941.

The history of ten pharmaceuticals has been told by Silverman in the form of stories about the men who made them available. The subjects range from morphine and quinine to the barbitals and sulfanilamide, and from the vitamins to the hormones. The author has left no "microbe's eyelash" unturned in his search for dramatic incidents, yet each narrative is true to the facts.

## SEX

REPORT OF THE COMMISSION ON MIXED MARRIAGES IN SOUTH AFRICA.

*Commission on Mixed Marriages, Union of South Africa. Government Printer, Pretoria.* 3s. 13 x 7⅝; 56; 1939 (paper).

The Commission was established to inquire whether marriages between Europeans and non-Europeans were (a) on the increase or likely to be, and (b) sufficiently numerous to be detrimental to the welfare of the Union, and "whether any further steps should be taken to discourage such marriages." Although the questions appear to the naive observer to be straightforward, this report concerns itself in great part with accounts of the miscegenation and immorality between the white settlers and the natives, the history of the marriage laws in the Union, and a summary of the marriage laws of the United States barring marriages between white and colored. So far as answering the above questions one is given a beautiful illustration of indirectness and prejudice. The official data on marriages between Europeans and non-Europeans show that there has been a decrease in such

unions. However, with justice the Commission points out that the data may not be accurate because some non-Europeans pass or are allowed to pass as Europeans. Therefore, no answer is given to question (a). Apparently the majority of the Commission voted yes to the first question under (b) mainly because miscegenation creates social problems. The Commission also voted yes to the second question. Exception to the Commission's conclusions was taken by one member, Mrs. Nellie Brown Spilhaus, M.P.C. She deserves to be mentioned because her comments, two pages long, represent a real attempt at an intelligent unbiased evaluation of the problem. If the Union of South Africa was seriously desirous of studying this important question it would seem that either the government or the local geneticists or both muffed the opportunity for some worth-while research.

THE WONDER OF LIFE. *How We Are Born and How We Grow Up.*

*By Milton I. Levine and Jean H. Seligmann. Simon and Schuster, New York.* $1.75. 8 x 5¼; 114; 1940.

This excellent presentation of modern sex hygiene is a tribute to the ingenuity of its authors—one a pediatrician and the other an educator. It has been written for preadolescents and adolescents in a clear, straightforward manner, avoiding all the sentimentality so often associated with books of this nature, and without offending the intelligence of its youthful readers. It gives clear, concise and simple descriptions of the male and female sex organs, the processes of puberty and related sexual changes, pregnancy, childbirth, and lactation. Additional chapters discuss twins, triplets, quadruplets, and quintuplets, family resemblances, and "the wonder of life." The illustrations and diagrams are particularly noteworthy and commendable. There is neither a bibliography nor an index, but a glossary of terms has been included.

## BIOMETRY

TABLES OF RANDOM SAMPLING NUMBERS. *Tracts for Computers No. XXIV.*

*By M. G. Kendall and B. Babington Smith. The University Press, Cambridge; Macmillan Company, New York.* $1.75. 9¼ x 6¼; x + 60; 1939.

This publication constitutes a supplement to No. XV of *Tracts for Computers* in which L. H. C. Tippett published a list of 40,000 "random numbers." The authors formed and tested for randomness 100,000 additional numbers. Since the numbers prepared by Tippett have proven their usefulness, the present series is a desirable addition to the statistical literature. Anyone who has the task of arranging any set of items in random order will find this publication useful. This reviewer has, in the past, found it advantageous to punch a number from Tippett's table on each Hollerith punched card carrying biometric data, in order that a random sub-set might be readily available. The longer series of random numbers will be very helpful in problems of this type.

THE BULLETIN OF MATHEMATICAL BIOPHYSICS. *Volume 3, Number 3, September, 1941.*

*Edited by N. Rashevsky. University of Chicago Press, Chicago.*

This number contains the following papers: Electrical Charges and Potentials in Cells Resulting from Metabolism of Electrolytes, by Robert R. Williamson; Note on the Mathematical Biophysics of Temporal Sequences of Stimuli, by N. Rashevsky; A Note on the Nature of Correlations Between Different Characteristics of Organisms, by N. Rashevsky; Mathematical Biophysics of the Galvanic Skin Response, by Clyde H. Coombs; A Theory of Steady-State Activity in Nerve-Fiber Networks: II. The Simple Circuit, by Alston S. Householder.

## PSYCHOLOGY AND BEHAVIOR

MIND THROUGH THE AGES. *A History of Human Intelligence.*

*By Martin Stevers. Doubleday, Doran*

*and Company, New York.* $3.75. 9 x $5\frac{3}{4}$; xii + 521; 1940.

Those who have read Ridpath's *History of the World* will recall that it consisted chiefly of lists of kings and battles. When this work was written in the last century kings were still considered the most significant personages in history, and battles its most decisive events. But a great deal of water has flowed under the bridge since Ridpath dropped his pen, as those who compare the present work, written a half-century later, may see for themselves. Today we realize that kings are mostly figure heads for "mayors of the palace," and that questions decided on the field of battle generally do not stay settled.

To the author of the work now under consideration it seems clear that the important events in human development have been thoughts. Whenever the course of history has been changed it is because somebody had an idea. The great revolutionaries have always been, and must always be, the great thinkers. To understand man it is necessary to understand what and how and why he thinks.

The present book is a history of human mentality. It begins with the origin of human intelligence, as nearly as that can be appraised on the basis of the psychology of babies, primates other than man, and our knowledge of the pleistocene submen. It then traces the development of intelligence through the archaeological and historical records to the present. In its pages we meet Hammurabi, Ikhnaton, Assur-bani-pal, Nabopolasar, and all the other thinkers of antiquity, as well as their successors and representatives in later ages, and learn just what they contributed to modern thought.

Four appendices cover respectively human raciation, the correlation of dates in ancient history and the establishment of those in pre-history, the growth of the alphabet, and the neolithic men of Europe, explaining in detail matters that are too often neglected in works of this nature.

The illustrations are good but they are altogether too few. The twenty-five page index is very comprehensive. The profundity of thought and the lucidity of its style combine to make this a truly great book that is likely to grip the reader's attention until he has read it from cover to cover.

PRINCIPLES OF ABNORMAL PSYCHOLOGY: *The Dynamics of Psychic Illness.*

*By A. H. Maslow and Béla Mittelmann. Harper and Bros., New York and London.* $3.50. $8\frac{1}{4}$ x $5\frac{3}{4}$; x + 638; 1941.

The foreword of this book states that it is an attempt

> to present an integrated picture of what we know of the psychologically disturbed individual. In this attempt we have used contributions from a wide variety of sources—from clinical, experimental, hypnotic, comparative, psychoanalytic, and psychobiological observations. Our aim was to avoid polemics and to utilize and synthesize whatever good material was available. We have brought to this task two traditions that are certainly ready for fusion, namely, the experimental-academic and the clinical-medical.

The book is divided into five parts. The first, Introductory concepts, concisely describes the present-day concepts of the "person as a whole," with adequate attention to complaints which may arise at any level of integration. The second part deals with psychodynamic processes which again are presented clearly with avoidance of technical language. The concepts presented deal with the individual in his attempts to make an adjustment to his environment. There is an interesting chapter on experimental behavior disturbances. The etiology of psychopathology is next discussed from the points of view of heredity, of cultural and social factors, and finally from the individual's own experiences, particularly in the parent-child relationship. In the section on therapy the various techniques commonly spoken of are described, with discussion of the methods and aims of each. The final section is a description of the various symptom syndromes, stressing Meyer's view of reaction types and pointing out the impossibility of rigid classification systems. The reactions are described in the conventional terminology with interesting case presentations.

There is a lengthy bibliography (819 references) in addition to the reference notes at the end of each chapter pointing

out the most pertinent references and the ground that each covers. Appendix I describes briefly various examination methods including the Rorschach test, play technique and the Murray thematic apperception test. A second appendix gives statistics bearing on the magnitude of the problem of mental disorder in the United States. The book is well indexed and contains a glossary.

STUDIES IN INFANT BEHAVIOR. *V. University of Iowa Studies in Child Welfare, Volume XVI, Number 2.*

*By Ruth K. Lederer and Janet Redfield. University of Iowa Press, Iowa City, Iowa.* $1.35 (cloth); $1.00 (paper). 9⅛ x 5¾; 157; 1939.

The first of the two studies which comprise this volume is concerned with the handed status of children during the first two years of life. A critical review of the literature forms an introduction to the body of carefully organized observations. Wherever possible, the data have been tested for statistical significance, and have been discussed in the light of such analysis. This investigation points to the general conclusions that: (1) between the sixth and eleventh month, there are about equal numbers of right- and left-handed cases; (2) changes in handed status occur more frequently during the first year of life than in the second; and (3) there is a tendency for changes to occur more frequently from left-handed status than from right. As a result of the exploratory nature of the investigation, the conclusions are admittedly tentative, requiring confirmation by further investigations along various suggested lines of approach.

The second study deals with the response of new-born infants to varying degrees of light intensity. In this, the accepted conclusion that light has an inhibitory effect upon the bodily activities of infants is confirmed, and is extended to include the observation that the inhibition is progressively greater as the intensity of light is increased.

Both studies are supplied with tabular matter and lists of bibliographic references.

THE PHILOSOPHY OF SILENCE.

*By Alice B. Greene. Richard R. Smith, New York.* $2.50. 8½ x 5½; xi + 254; 1940.

The author of this book states that her purpose has been "to examine into the practice of silence as observed in many different climes and times, and to do this in the scientific spirit. . . ." She states: "Much is required of . . . the aspirant to first-hand knowledge of the wider reaches of his own being and the larger realities to which it can lead." This statement suggests the, what seems to this reviewer, unfortunate dichotomy which pervades the book, namely the "supernormal experiences" of man in contrast to his materialistic satisfactions. Two types of silence are recognized—reflection of scientific thinking which is usually concerned with external problems, and religious meditation which attempts to push back "inner frontiers" and the "invisible sources" of life—"the larger life," "rebirth," "transformation of the self," etc. The author states: "The practice of the religious type of silence necessitates a progressive stilling of the physical, emotional and mental areas . . . a cleansing of subconscious areas." It is to this latter type of silence that eight of the ten chapters of this book are devoted. The material assembled is largely historical and was gathered in preparation for the author's doctoral thesis at Columbia University. The handling of the subject matter is in the evangelistic rather than scientific spirit. There is a bibliography and an index.

THE ADOLESCENT PERSONALITY. *A Study of Individual Behavior.*

*By Peter Blos. D. Appleton-Century Company, New York and London.* $3.00. 8⅜ x 5⅜; xiii + 517; 1941.

This book presents a study of adolescents which is of great interest both in itself

and in the concepts delineated. It is essentially a study of personality reactions as reflected in the individual's performance record and his behavior under different circumstances, with emphasis on the meaning of what he says and does in the light of his personality organization. The approach used is that of the case-study. The book is divided into five sections. In the first section certain fundamental concepts are given and the case-study approach is discussed. In the second section two case studies, one of an adolescent school-girl and one of an adolescent school-boy, are presented in detail. Based on this type of material, a theory of adolescent development is discussed in the third section. The goals of adolescence are formulated as three-fold: emancipation from the family, heterosexual adjustment, and vocational, ideational, and economic self-determination. Adolescent behavior is seen as experimental and protective in character, bearing the signs of temporary adaptive efforts toward these goals. In the fourth section two case studies of an out-of-school adolescent girl and boy are given. The final section is devoted to a discussion of education and adolescent development.

A list of references is given at the end of sections one, three, and five, and there is an index. A sound, factual, thought-provoking contribution to the literature on adolescence.

THE NINETEEN FORTY MENTAL MEASUREMENTS YEARBOOK.

*Edited by Oscar K. Buros. Mental Measurements Yearbook, Highland Park, N. J.* $6.00. Ten percent discount given on all orders sent directly to the Mental Measurements Yearbook. 10½ x 7½; xxiii + 674; 1940.

This book represents a very complete and successful attempt by 250 of the leading psychologists, teachers, and test technicians to review the huge numbers of tests available for measuring various human qualities and abilities. The reviews are frankly critical and one is given definite indication of what value the reviewer considers the test and what its use should be. The subject matter covers tests on character and personality, achievement batteries, educational subjects such as languages and mathematics, a miscellaneous section having to do with such widely diversified interests as religion and agriculture, science, social studies, and vocations. To this mass of material is added a collection of various reviews that have been accorded books related to this general subject during the past year. These are instructive and very interesting as the opinions are often sharply conflicting. The price of each test and book and where it may be obtained is added.

In the section on character and personality tests there is an excellent bibliography concerning the Rorschach test but nothing concerning the test itself. One also misses reference to Murray's thematic perception test, a test which is coming more and more into clinical use.

A FIELD STUDY IN SIAM OF THE BEHAVIOR AND SOCIAL RELATIONS OF THE GIBBON (HYLOBATES LAR). *Comparative Psychology Monographs, Volume 16, Number 5, Serial Number 84.*

*By C. R. Carpenter. With an Introduction by A. H. Schultz. The Johns Hopkins Press, Baltimore.* $2.00. 10 x 6¾; 212; 1940 (paper).

This monograph presents a graphic account of a field trip made by the author over a four-month period in 1937 to Siam to study the gibbon in its natural habitat. The project is described as "a systematic naturalistic study by observational and recording methods of the ecology, behavior and social relations of the gibbon, *Hylobates lar*, in its natural environment in Siam." The material comprised in this monograph is presented in precise and interesting fashion. In the introduction the place of the gibbon among the primates is discussed by Adolph H. Schultz. Chapter I describes the objectives and organization of the expedition

itself. In the following chapters observations made on individual behavior, population, intragroup social relations, territoriality and inter-group relations, and group coordination, control and integration are reported. The final chapter contains a general summary of the main points noted. There is a bibliography of 103 titles and an index.

COURTSHIP AND DISPLAY AMONG BIRDS. *By C. R. Stonor. Country Life, Ltd., London.* 8s. 6d. net. $8\frac{5}{8}$ x $5\frac{3}{8}$; xv + 140; 1940.

Birds are well known to have spectacular and intricate displays of infinite variations, each species with its own individual pattern. To describe all these performances would be impossible in anything but a monumental compendium. The author has therefore chosen some of the more complex and better known displays for those interested in natural history and for ornithologists who have not had time to go deeply into this branch of the subject.

Stonor believes that form preceded function and arose by variations that were selected for their greatest use and that these were converted through the ages to their present form. This idea he illustrates by examining closely the behavior of several closely related birds (the birds-of-paradise) and correlating differences in their behavior pattern with their morphological peculiarities.

The illustrations are excellent and show to what extent bird photography has progressed. Altogether this is a good review of a complicated phase in the behavior of birds and should be of interest to all biologists.

THE PERSONALITY OF ANIMALS. *By H. Munro Fox. Allen Lane, Penguin Books, Harmondsworth.* 6d. 7 x $4\frac{1}{4}$; 123; 1941.

Most of us, in expressing opinions about the minds of animals, assume that the animal's mentality is a simpler edition of our own. The scientist, however, will permit himself to assume nothing; he investigates the animal's mind just as he does the animal's breathing or digestion—by experimentation. In the present book, Fox gives, in clear and non-technical language, the biologist's point of view on the senses, the mind, and the personality of animals, together with the most important recent results of scientific investigations. Subjects discussed include: the animal's world; how animals communicate; what some animals can hear and what colors they can see; play; animals that find their way home; can animals count?; social rank, instinct; and intelligence. The conclusion reached is that "those animals which have the fewest instincts possess most personality." The series of sixteen illustrative plates is very well chosen. The book contains neither bibliography nor index.

A WATERHEN'S WORLDS. *By Eliot Howard. The University Press, Cambridge; The Macmillan Company, New York.* $2.50. 10 x $7\frac{1}{4}$; vii + 84 + 2 plates; 1940.

From careful observations of the breeding habits of the waterhen, the late Eliot Howard again demonstrates his keen analytical interpretations of animal behavior. The worlds of the waterhen are said to consist of the territory world, the sexual, the platform, and the family. These worlds are not separate entities, but form part of a connected whole, and, in the breeding cycle, necessarily follow in chronological order. Howard feels sure that birds have feelings that are expressed in action but that these two are concomitant as there is no feeling without action and no action without feeling. The internal physiological state of the individual which changes from day to day, has a bearing on the bird's activities.

This book is recommended only to a serious reader for it is not easy to follow the author's argument. It is a notable contribution by a great observer who was

a pioneer in the modern study of bird behavior.

## DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

RELIGION IN SCIENCE AND CIVILIZATION. *By Sir Richard Gregory. The Macmillan Company, London and New York.* $3.00. 8½ x 5¼; xiii + 366; 1940.

The author of this work tells us that religion, like Gaul, is divided into three parts—theology, worship, and ethics. The first of these to emerge in human evolution was worship, which originated as a ritual of taboos for the purpose of coercing the personified forces of nature to do the will of the worshippers.

From such humble beginnings came the exalted ethical teachings of Zarathustra, of Lao-tse, of Buddha, of Jesus. These bodies of doctrine did not appear miraculously like Melchisadek, without ancestry, but came about as the ultimate fruition of the perpetual striving of the genus *Homo* to pierce the veil of the temple of nature—a striving that is firmly rooted in the fetishism and animism of the paleolithic cave man.

The teachings of such intellectual leaders constitute ethics, but the systems of belief that accumulate about the memory of them constitute theologies, and it is with theologies that this author is chiefly concerned. He traces the evolution of the various components of contemporary Christian thought from Sumerian and later aboriginal sources to the present.

The author is particularly happy in his treatment of the cultural aspects of warfare. In a very timely discussion he points out that it is to the defeated and conquered Athenians, and not to the victorious Spartans, that everything good in Greek civilization is due. The militarism that won the war for Sparta also precluded that state from making any substantial contribution to Greek culture, and to the pacifism that brought about its defeat on the field of battle Athens owes its immortality. The lesson seems to be that pacifism is the most practical course for a people who wish to leave an indelible imprint on the civilization of coming ages.

A peculiar feature of the work is a consistent tendency to assign pre-Christian era events a date one year later than that commonly accepted by authorities. Apparently this is an attempt to supplant the illogical chronology to which historians are addicted by the more exact system used by astronomers. The contiguity of the years one B.C. and one A.D. in historical chronology is due to the accident that when Dionysius Exiguus devised the method of dating events from the Nativity there was as yet no zero in the European mathematical scheme. The attempt to restore the zero year as astronomers have done is altogether laudable, and the author deserves congratulations for his courage.

The index covers only ten pages, which is quite inadequate for the wealth of material between the covers of this book, which is exceedingly well written and highly stimulating.

CLASSIFIED INDEX TO THE PUBLICATIONS OF THE AMERICAN PHILOSOPHICAL SOCIETY, 1769–1940.

*American Philosophical Society, Philadelphia.* Free. 8¼ x 5½; v + 173; 1940 (paper).

During the long career of the American Philosophical Society (in another two years it will celebrate its two hundredth anniversary) many important papers and communications reporting advances in science and in thought in America have been reported at its meetings. In its very early years the Society issued no printed records but in 1769 *The Transactions*, now the oldest scientific journal in America with a continuous history, appeared. The first six volumes (old series) were in small quarto format. In 1818 a new series, the present large quarto format, was started and to date, 31 volumes have been published. *The Proceedings*, containing original papers read before the society and others accepted for publication, also abstracts, and verbal communications and letters on scientific and learned subjects (of special interest to research students

and historians), first made its appearance in 1838. It was not until 1935 that the *Memoirs*, consisting of monographs of book length, each constituting a separate volume of the series, was started. Other publications are the *Year Book* and *Miscellaneous Publications*. In the present list, papers and books are classified under fifty headings, ranging through all branches of the sciences, and literature, philosophy, languages, politics, biography, and exploration. On a rough estimation, we place the number of items at about 3500. Many of the early papers are out of print, but the Library maintains a Photoduplication Service and for a nominal sum will furnish copies of out-of-print articles and manuscript material.

A price list follows the classified list—there is no attempt to push prices upward—and an index of author's names concludes the catalogue. Anyone desiring to enrich his library would do well to study this catalogue with care. It will yield many desired items.

FROM BEAST-MACHINE TO MAN-MACHINE. *Animal Soul in French Letters from Descartes to La Mettrie.*

*By Leonora C. Rosenfield. Oxford University Press, New York.* $3.50. 8½ x 5¼; xxviii + 353; 1941.

This is the history of a strange idea, held but little nowadays—that the animal body is a mechanism in the strict sense. Not merely that the motions of the body take place in accordance with the laws of mechanics, for that is quite obvious, but that consciousness itself is only a function of material organization and must not be postulated except when verified by experience. Even the construction in the remote future of robots actuated magnetically to do all that a man can do is not an impossibility. The doctrine seems to have originated with Descartes, who went through a stage of materialistic thinking in his youth. Later when the great French philosopher admitted the existence of the human soul, the doctrine of the kinship of man to the rest of the animal kingdom had become repugnant to the ecclesiasts, and Descartes found it expedient to continue to regard the subhuman animals as automata, without power to feel or to think.

La Mettrie, on the other hand, was a medical man, capable of appreciating man's systematic position among the animals. But being under no obligation to the ecclesiasts he accomplished his synthesis of the animal kingdom not by recognizing the animal soul but by denying the human soul. It is true that he was not always consistent—what philosopher is?

The author presents a scholarly analysis of the doctrines of these two writers and a host of others between them, and has provided an extensive documentation and an exhaustive index.

THE SOCIAL ROLE OF THE MAN OF KNOWLEDGE.

*By Florian Znaniecki. Columbia University Press, New York.* $2.50. 7¾ x 5¼; 212; 1940.

How has the seeker after knowledge, the scientist or, more precisely, the savant attained his present position in our society? This is the question that Znaniecki attempts to answer in this monograph which summarily describes the processes of social interactions involving the cultivator of knowledge. The author apparently views these processes in the form of a gradual evolution of individual ideation and of group consciousness. At first the individual technical skill and interest is dedicated to the narrow field of immediate practical needs, then the individual advances beyond the needs or expectations of the social group. He becomes the technological inventor. Similarly with respect to so-called spiritual needs the sage emerges into the scholar and later the "scientific explorer." While the technologist and the sage acquired elevated social standing because they coupled knowledge with authority, "scientists came to be socially accepted because and in so far as they specialized in cultivating a kind of knowledge which men of action regarded as useful for practical purposes." Scholars have assumed their social position because they have

convinced others and are themselves convinced that knowledge gives power "because and only because it is pure theory, an objective system of truths, and man must know reality truly in order to control it effectively." The author has obviously only begun to probe the question, nevertheless this exposition will interest all scholars and scientists and is a contribution to a sociology of knowledge.

TEMPERATURE MEASUREMENT.

*By Robert L. Weber. Edwards Brothers, Inc., Ann Arbor, Michigan.* $2.50. $10\frac{3}{4}$ x 8; x + 171 + [6]; 1941 (paper).

"It is the purpose of this book to outline an experimental study of the methods of temperature measurement with the theoretical principles necessary for their appreciation, intelligent use and extension."

The principles involved are presented in Part I. This includes concise discussions of the theoretical, and descriptions of the practical, methods used in expansion and resistance thermometry, thermoelectric and radiation pyrometry, recording of temperatures, automatic temperature control, colorimetry, and measurement of extreme temperatures. Further theoretical sections deal with thermal analysis and elementary thermodynamics. In addition to a list of problems designed to familiarize the student with this highly technical subject, the second part of the book is devoted entirely to experiments illustrating the principles previously described. An extensive appendix contains tables of physical constants, temperature conversion, and thermocouple characteristics for various metals.

Besides being a well organized and useful text, this book should find widespread acceptance in many fields of scientific and industrial research.

THE MICROSCOPE.

*By R. M. Allen. D. Van Nostrand Company, New York.* $3.00. 9 x $5\frac{3}{4}$; viii + 286; 1940.

From its early use by amateur enthusiasts, the microscope has steadily increased in importance until at present it is an indispensable tool not only in the various phases of biology, but also in other sciences and industry. All too few people who must use this instrument fully understand its principles, thus impairing the quality of their work. The author has outlined these principles and methods of handling the microscope in the clearest possible terms, so that even those without training in optical science will become better acquainted with the microscope by reading this book. A chapter on the history of the microscope is followed by discussions on optical principles, descriptions of lenses and various mechanical devices of modern microscopes, and instructions in the use of the microscope, including illumination and techniques of preparing material for microscopic study.

INTRODUCTION TO LOGIC *and to the Methodology of Deductive Sciences. Enlarged and Revised Edition.*

*By Alfred Tarski. Translated by Olaf Helmer. Oxford University Press, New York.* $2.75. $8\frac{3}{8}$ x $5\frac{1}{2}$; xviii + 239; 1941.

The Greeks were the great logicians of antiquity but they were not mathematicians, and consequently their logic lacked the precision and exactitude demanded by a world of non-Euclidean geometries and relativity physics.

The present work is intended to supply this lack, and is based on mathematical axioms and expressed in mathematical formulae. It will doubtless succeed eventually in supplanting the classical logic of the trivium. It is intended for use as a text book, and is well provided with exercises. Also it has a bibliography and an index, both of which are quite comprehensive.

HOW TO BUILD AND EQUIP A MODERN DARKROOM.

*By Nestor Barrett and Ralph Wyckoff. Camera Craft Publishing Company, San Francisco.* $2.00. 8¾ x 5¾; 133; 1940. Many amateur photographers spend large sums of money on equipment for taking good pictures and then produce only mediocre work because of an inadequate darkroom. Detailed descriptions are given in this book for building a good photographic laboratory which will be adaptable to basement, attic, or apartment. Prices are included so that the individual may plan within his budget. Surfacing, ventilation, lighting, plumbing, and accessories are all thoroughly discussed and diagrammed. A supplementary chapter describes a home motion-picture auditorium for advanced enthusiasts. Many time- and money-saving ideas are incorporated in these pages.